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L.M.B.C. MEMOIRS

ON TYPICAL BRITISH MARINE PLANTS & ANIMALS

EDITED BY W. A. HERDMAN, D.Sc., F.R.S.

XVIII.

ELEDONE

BY

ANNIE ISGROVE, M.Sc.

(With 10 Plates)

PRICE FOUR SHILLINGS AND SIXPENCE

LONDON
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JULY, 1909

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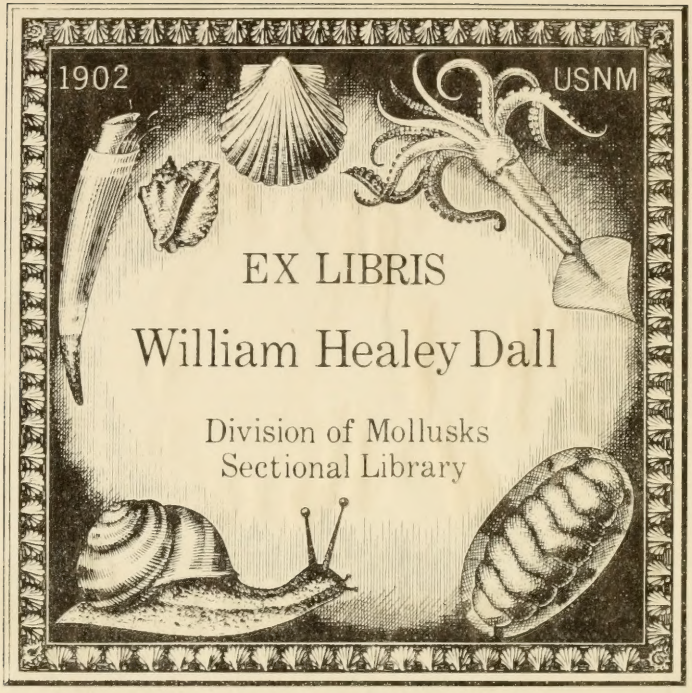
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XVIII.

ELEDONE.

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EDITOR'S PREFACE.

The Liverpool Marine Biology Committee was constituted in 1885, with the object of investigating the Fauna and Flora of the Irish Sea.

The dredging, trawling, and other collecting expeditions organised by the Committee have been carried on intermittently since that time, and a considerable amount of material, both published and unpublished, has been accumulated. Twenty-two Annual Reports of the Committee and five volumes dealing with the "Fauna and Flora" have been issued. At an early stage of the investigations it became evident that a Biological Station or Laboratory on the sea-shore nearer the usual collecting grounds than Liverpool would be a material assistance in the work. Consequently the Committee, in 1887, established the Puffin Island Biological Station on the North Coast of Anglesey, and later on, in 1892, moved to the more commodious and accessible Station at Port Erin in the centre of the rich collecting grounds of the south end of the Isle of Man. A larger Biological Station and Fish Hatchery, on a more convenient site at Port Erin, has since been erected, and was opened for work in July, 1902.

In these twenty-two years' experience of a Biological Station (five years at Puffin Island and seventeen at Port Erin), where College students and young amateurs form a large proportion of the workers, the want has been frequently felt of a series of detailed descriptions of the structure of certain common typical animals and plants, chosen as representatives of their groups, and dealt with by specialists. The same want has probably been felt in other similar institutions and in many College laboratories.

The objects of the Committee and of the workers at the Biological Station were at first chiefly faunistic and speciographic. The work must necessarily be so when opening up a new district. Some of the workers have published papers on morphological points, or on embryology and observations on life-histories and habits; but the majority of the papers in the volumes on the "Fauna and Flora of Liverpool Bay" have been, as was intended from the first, occupied with the names and characteristics and distribution of the many different kinds of marine plants and animals in our district. And this faunistic work will still go on. It is far from finished, and the Committee hope in the future to add still further to the records of the Fauna and Flora. But the papers in the present series, started in 1899, are quite distinct from these previous publications in name, in treatment, and in purpose. They are called "L.M.B.C. Memoirs," each treats of one type, and they are issued separately as they are ready, and will be obtainable Memoir by Memoir as they appear, or later bound up in convenient volumes. It is hoped that such a series of special studies, written by those who are thoroughly familiar with the forms of which they treat, will be found of value by students of Biology in laboratories and in Marine Stations, and will be welcomed by many others working privately at Marine Natural History.

The forms selected are, as far as possible, common L.M.B.C. (Irish Sea) animals and plants of which no adequate account already exists in the text-books. Probably most of the specialists who have taken part in the L.M.B.C. work in the past will prepare accounts of one or more representatives of their groups. The following list shows those who have either performed or promised.

Memoirs from I. to XVIII. have now been published.

The next, on Polychaet Larvæ, by Mr. F. H. Gravely, is now in the press; Doris, by Sir C. Eliot, is far advanced and ought to be out during 1909. It is hoped that Cucumaria, Buccinum, and the Oyster will follow soon.

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Himanthalia, F. J. Lewis.
Diatoms, F. E. Weiss.
Fucus, J. B. Farmer.
Botrylloides, W. A. Herdman.
Actinia, J. A. Clubb.
Hydroid, E. T. Browne.
Halichondria and Sycon, A. Dendy.
Sabellaria, A. T. Watson.

In addition to these, other Memoirs will be arranged for, on suitable types, such as *Pagurus*, *Pontobdella*, a Cestode and a Pycnogonid.

As announced in the preface to Ascidia, a donation from the late Mr. F. H. Gossage, of Woolton, met the expense of preparing the plates in illustration of the first few Memoirs, and so enabled the Committee to commence the publication of the series sooner than would otherwise have been possible. Other donations received since from Mrs. Holt, Sir John Brunner, and others, are regarded by the Committee as a welcome encouragement, and have been a great help in carrying on the work.

W. A. Herdman.

University of Liverpool,
June, 1909.

L.M.B.C. MEMOIRS.

No. XVIII. ELEDONE.

(The Octopod Cuttlefish.)

BY

ANNIE ISGROVE, M.Sc.

PREFACE.

The greater part of the work for this Memoir has been done in the Zoological Research Laboratory of the Manchester University. I take this opportunity of thanking Professor Hickson and Mr. Hewitt, of that University, for their helpful suggestions. Dr. Hoyle, of the Manchester Museum, also kindly lent me much of the literature of the subject, and assisted me in various ways. My thanks are due to the Council of the Marine Biological Association of Great Britain for the use of a table at the Plymouth Laboratory, during the Easter vacation, 1908, and also to Mr. Chadwick of the Port Erin Biological Station, for several useful notes with which he supplied me as to the occurrence of *Eledone cirrosa* in that district, its habits, method of capture and other details.

INTRODUCTION.

Eledone cirrosa (Lamarck, 1798), or *Moschites cirrosa*, as it should be called according to the rules of the International Zoological Congress, belongs to one of the two genera of British Cephalopoda Octopoda. The following table, showing the classification adopted in Pelseneer's Text Book, illustrates the relation in which *Eledone* stands to other groups of Cephalopoda :—

Class Cephalopoda.

1. *Sub-class* Tetrabranchia, e.g. *Nautilus*.
2. *Sub-class* Dibranchia.

Order I. Decapoda, e.g. *Sepia*.

Order II. Octopoda.

Family Octopodidae—*Genus* Eledone.*

All Cephalopoda are aquatic marine animals. The genus *Eledone* occurs in the Mediterranean, round the Atlantic coasts of Europe, and elsewhere. *Eledone cirrosa* is the species confined to British waters, and is the only British representative of the genus. To the other British genus *Octopus*, belong *O. vulgaris* the common "Octopus," and *O. arcticus* a smaller deep-sea form.

Eledone cirrosa has been chosen for this Memoir because it is a convenient type for dissection, and may be fairly easily obtained at the Plymouth and Port Erin Biological Stations. It has also a certain economic importance, feeding on crabs and lobsters, and often extracting them from the crab and lobster pots put out by the fishermen. Popularly *E. cirrosa* is known as "the

* As shown by Dr. Hoyle (Manchester Memoirs, Vol. XLV, No. 3, 1901, the correct generic names for "Octopus" and "Eledone" are *Polypus* and *Moschites* respectively. Hence the true title of *Eledone cirrosa* is *Moschites cirrosa*. Yet, as the names *Octopus* and *Eledone* have been in general use for 100 years or more, I think it on the whole better to continue to use them.

lesser Octopus," as it never attains the size of the common Octopus. It is also distinguishable by the single row of suckers on each arm.

Occurrence.

During the spring, Eledone is brought in from depths of 30 to 35 fathoms, at Plymouth and Port Erin, by trawlers and other fishermen. At this season, young specimens have also been taken occasionally in a few inches of water, at low water of spring tides, at Port Erin. The Eledones brought up in the trawl are probably caught while adhering to or creeping over stones and rocks, or while swimming near the sea bottom. They seem to occur in small groups of two to six in number. At Port Erin and Plymouth they are also taken in crab and lobster pots. These, at Port Erin, are put out at depths of from six fathoms inside the bay to twelve fathoms outside it. Although Eledone is always fed on Crustacea, when kept in captivity, and careful examination of about fifty specimens has shown no other than Crustacean food in the gut, yet occasionally at Port Erin, the fishermen have taken Eledone on hand lines baited with pieces of herring and mackerel. The mouths and oral surfaces of such specimens are lacerated by the hook, showing that the Eledones actually attack the bait.

During the winter Eledone leaves the shallow water, round the South coast of Devonshire, and seeks the warmer and deeper water in the centre of the channel. Specimens taken in this season, from deep water, generally die before the trawlers get back, probably from cold. With the warmer months Eledone comes further in, and so from May to September it is taken in Plymouth Sound, at an average depth of eight fathoms; and in a hot summer it is unusually abundant. Some-

times it is found stranded at low tide, in the rock pools on various parts of the coast. Curiously enough, the Eledones obtained are almost always females. The relative abundance of the sexes appears to be fifty females to one male. This disparity in proportion is also noticeable to a greater or less degree in all Cephalopods. Possibly the males, besides being fewer in number, remain in deeper water, the females alone coming in with the warmer weather to spawn, or, again, the males may have a different method of concealment.

Habits.

Eledone cannot be called an active animal. When kept in a tank, if undisturbed, it passes most of its time resting. Its attitude is often, as Text fig. 1 shows, with the arms bent at an acute angle to the body, and adhering to the floor of the tank by the suckers on the proximal regions of the arms. The visceral dome also rests postero-ventrally on the ground, and the eyes are more or less closed. At other times it rests with the tentacles folded together so as to form an oval disc of attachment by which it clings to the wall of the tank, the body hanging downwards in the water.

When disturbed, Eledone seeks to escape by swimming rapidly backwards, the motion being obtained by ejecting powerful jets of water forward from the anterior opening of the funnel. When swimming, the arms are stretched out horizontally in a straight line with the rest of the body, while the visceral dome points forwards. The eight arms lie closely together, and looking down on the animal from above, six arms may be seen. Of these the outermost pair—II ventral—are curved outwardly in the middle region. Thus Eledone does not use the web when swimming, but only when

sinking downwards through the water. Then the tips of the arms separate radially like the ribs of an umbrella, so as to stretch out the triangular pieces of web between the arms.

Eledone has another mode of progression—creeping. This it does with a gliding motion, sometimes slowly, at other times more rapidly—particularly when in pursuit of food. When creeping, the body is raised from the floor of the tank, and the animal advances somewhat in the posture of the Text fig. I, creeping by means of the suckers on the middle region of the arms. Sometimes

Fig. I.—*Eledone cirrosa*, at rest.

the suckers further down are used, and consequently the body is raised higher, while the animal appears to advance on tip-toe. Eledone generally creeps thus when stalking prey. Often when creeping up the wall of the tank, the arms are well separated, so that the web is half extended. Apparently, Eledone only swims when seeking to escape. Possibly when not in captivity it may have nocturnal periods of activity, when swimming takes place. Careful watching of active specimens has not, however, revealed this habit, but that may be explained, perhaps, as due to artificial conditions.

During the night Eledones will sometimes escape by climbing over the walls, if in an uncovered tank.

The shape of the visceral dome varies considerably. When resting, the body is shortish, and forms a bluntly rounded stout sac, and the arms may be coiled up or stretched out, and are often waved gently about; while at other times they are passed over the surface of the body, seeming to brush it, or are passed down into the mantle cavity and then out again. When swimming, however, the shape of the body alters. It becomes stretched out antero-posteriorly, and so assumes a form very like that of *Sepia*, while a lateral fold of skin becomes prominent, which marks off the dorsal from the ventral surface, and forms a delicate fin, very similar again to that found in *Sepia*. Wave-like undulations, beginning at the front and passing backward, pass along this temporary balancing organ, which helps to support the body. With the return to rest or creeping the fin is lost again, becoming indistinguishable from the general body surface. Also when swimming, a longitudinal median depression on the ventral surface of the mantle indicates the line of insertion of the vertical septum, on its inner surface.

Eledone is often found in the morning adhering halfway up the glass front of the tank, nearest the light. At other times it hides in dark corners, and if stones are provided, will heap these into a rough mound in a corner of the tank and hide behind this. It was, no doubt, this desire for dim seclusion that often led one to rest with the cephalopedal mass inside a jam jar, which was in one corner of the tank. Eledone, apparently, dislikes a strong light, in which it seems quite incapable of opening its eyes. If a light is brought near during the night, the eye contracts and the animal retreats.

How long Eledone lives is not known. However, from the fact that during the early spring quite young specimens occur—probably hatched from the previous summer's spawn—together with many stages between half and full grown specimens, they probably live several years under natural conditions. At present nothing is known as to their rate of growth, or the size at which sexual maturity is reached. Eledone is an extremely delicate animal, and rapidly suffers if the tank in which it is placed has not a good and constant supply of sea water. Hence it is practically impossible to observe it alive elsewhere than at the Marine Biological stations. Confinement affects it in various ways. For instance, although it was found, on dissecting several Eledones which had been kept in captivity for some weeks, that the ink sac was full of ink; yet after the violent ejection of ink which occurred when the animals were first caught, and one or two very slight subsequent discharges, no ink was ever again poured out. Even when being killed, no ink was ejected, although the body was convulsed, and the animal appeared to make a great effort to discharge the secretion.

Food.

As Eledone is taken in both crab and lobster pots, probably it eats both these Crustaceans. However, when kept in tanks, it is generally fed on crabs, and crab remains alone were found in the gut of numerous specimens which were examined. It has been known to attack and devour the Norway lobster, and will take prawns or shrimps when they are placed in the same tank. Preferably it takes the Edible Crab, *Cancer pagurus*, but *Portunus depurator* is also taken, and *Carcinus moenas*. Eledone sometimes stalks its food, creeping after the

scuttling crabs in the posture previously described. With a quick rush it generally reaches its prey and renders it incapable of motion by spreading its arms over the crab. Sometimes it gathers up several crabs simultaneously in this way—taking an armful as it were. These are then consumed one by one. At other times it secures its prey by quickly swooping down upon it from the water above, with the arms outstretched.

How, exactly, Eledone opens the crab cannot be seen, as the arms cover over and so hide the prey from view when it is being consumed. If, however, the dorsal carapace is removed from a crab in the easiest way possible, beginning at the posterior edge, and simply pulling the shell away, the portion which comes away is exactly similar in shape to that which Eledone leaves. Hence probably it adopts this method of removing the carapace with its beak, and then eats the soft body of the crab. Usually the ventral exoskeleton and limbs of the victim are left attached to one another, or the limbs may be broken away. While feeding, Eledone curls its arms about in the water, as though with pleasurable excitement. No accurate observations have been made as to the amount of food consumed in any given time. They have been known to attack and eat one another, the arms only of the victim, which is not necessarily killed, being generally devoured. Only two records have been made of the occurrence of *E. cirrosa* in the stomach of British fish (the Angler and the Ling—see list below). It is not improbable that dolphins and porpoises prey on the large Eledones, while the young and therefore small and feeble ones probably form food for various marine animals. When they attain some size, the suckers and beak will render them decidedly uninviting. Possibly their sinister attitude and bright colour also protect them. Congers

will take pieces of the flesh when given as food, but other fish refuse it altogether. Crabs will take it as food only reluctantly, although they will readily eat weak or dead Sepia.

Cephalopods have been recorded as follows from the stomachs of British fishes:-

Loligo, in Cod, Whiting, Gurnard, Plaice, Skate.
Octopus, in Haddock, Ling, Whiting, Plaice.
Eledone, in Ling and Angler. (Two isolated cases only.)
Rossia, in Haddock, Whiting, Cod, Gurnard, Dab, and Long Rough Dab.
Sepiola, in Whiting, Cod, Gurnard, Tope, Thornback, Dab, and Pout.

EXTERNAL FEATURES.

I.—Skin.

The skin of Eledone has a smooth external surface. It is soft and slimy to the touch, and contains numerous gland cells. These secrete an opaline mucus, which is especially noticed while killing the animal, say, with chloroform, when the body becomes coated with this secretion. It is, however, by no means as thick or sticky or as abundant as that secreted by *Archidoris*, or the common garden slugs, under similar conditions. In appearance the skin is smooth and velvety, and reminds one of a peach. It is also tough and elastic. When Eledone is quiet it may be noticed that the skin is finely granulated all over the body. In addition to these granulations, there are also larger conical processes or cirri, on the head and back, of 6 to 12 mm. in height.

On the head there is a single pair of these cirri, which remind one of slight horns, over the eyes (Pl. I, fig. 1, *l.d.c.*), and down the back there are about seven rather irregular rows of five or six papillae. However, when Eledone is agitated or moving about, the skin appears to become tightened over the surface of the body, and this stretching causes the granules and cirri to flatten down, and become indistinguishable from the rest of the surface. After a short period of rest, the slackening of the skin causes the granules and cirri to reappear. These processes are not visible after death, and so a true idea of the skin of Eledone can only be gained by watching the living animal.

The colouration of the body is due to the chromatophores which lie in the dermis, and are only absent from (1) the oral surface of the web, and (2) the suckers and the oral surface of the basal parts of the arms. Hence these parts are white, but when the web is stretched open, the chromatophores on its aboral side may be seen through as greenish dots, by transparency. The following notes were made as to the colouration of Eledones kept in the tanks of the Plymouth aquarium, when undisturbed:—

1. Lower or ventral aboral surface of web light buff, with a pale green metallic tinge.

2. Dorsal aboral surface of web buff mainly, with flecks of cream scattered in between the predominating patches of buff; aboral surface of arms similar.

3. Funnel light and practically colourless posteriorly, with yellowish-brown colouration anteriorly. The colour is deeper on the dorsal than on the ventral surface of the funnel, where there is also some indication of the metallic green tinge which is found on the ventral surface of the web, and of the mantle sac.

4. On the ventral surface of the mantle sac the brownish chromatophores are larger than in other parts of the mantle, and situated further apart. The prevailing colour here is white, with a light, metallic green cast.

5. The dorsal surface of the visceral dome, like that of the web and head, shows patches of cream in between large flecks of a reddish-buff colour. From the eyes two oblique lines of cream colour slant inwards and meet, forming a light-coloured **V** on the dorsal surface of the head. The iris of the eye is deep orange in colour. The chromatophores are continued over the free edge of the mantle, for about half an inch inside the pallial cavity. The marbling of the skin is most distinct when the animal is recovering from excitement. When quiet the cream and buff flecks fade into one another rather indistinctly, while the intense blush caused by excitement spreads all over the skin and temporarily eliminates the marbling, but when recovering again, the cream flecks show up well against the terra-cotta patches. When the animal is excited the skin becomes of a very dark reddish terra-cotta tinge. After death the eyes become dull, and the skin loses its velvety gloss and beautiful colouration utterly, and becomes overcast with a dull grey tinge. When Eledone is frightened in any way, the skin changes colour, and an intense pallor spreads over it, causing it to become quite ghostly in appearance. At this time the eye stands out very prominently, because the iris remains dark orange, as does the eyelid surrounding it, and thus an orange circular patch marks out the eye, on a whitened body. However, under normal conditions this patch does not stand out in any way. At the same time that the pallor is seen the animal tries to escape by rapidly swimming backwards, and attempts to eject ink. Almost immediately the pallor is replaced by an intense

darkening or blush of deep terra-cotta colour over the whole body. If allowed to come to rest again now, the colour gradually lightens until the normal condition is reached. If the animal is stimulated several times in succession say by poking with a glass rod, or by bringing a brightly coloured bottle near—it becomes exhausted, the pallor becomes less intense, and the consequent darkening less noticeable; also efforts to escape cease. At night the colour is like that of the resting condition.

Structure of the Skin.—The skin consists of a columnar epidermis, and a subjacent and much thicker dermis (Text fig. II). It may easily be detached from the muscular body wall, thus destroying the deeper layers of the dermis. The epidermal cells secrete a thin cuticular protective layer externally, while internally they are each produced into several fine processes which attach the epidermis closely to the dermis.

The dermis is divisible into four layers, as follows:—

1. External fibrous layer (Text fig. II, *Ex.C.L.*).
2. Layer with chromatophores (Text fig. II, *Chr.*).
3. Layer containing iridocysts (Text fig. II, *Irid.*).
4. Internal fibrous layer. This is the thickest layer, and connects the skin to the underlying muscles of the body wall. It contains the vessels and nerves of the skin, and also feeble muscular strands (Text fig. II, *I.C.L.*).

Chromatophores.—These are extensible pigment-containing vesicles, occurring in the external part of the dermis (Text fig. II, *Chr.*). Their expansion and contraction cause the changes of colour so characteristic of all Dibranchiate Cephalopoda. The origin, structure and movements of the vesicles have been studied by many people, and much variation of opinion exists on all three points. The views of Rabl, Müller, Klemensiewicz, Frédéricq and Kölliker may be briefly summarised thus:

1. The central spherical cell, which contains pigment granules, is a uninucleate cell which originates in the epidermis and later sinks down into the dermis. The cell wall is a tough elastic membrane, and the pigment granules are arranged round the periphery of the cell, leaving the central protoplasm clear.

2. A girdle of about 18 mesodermal cells becomes grouped round the equatorial region of the pigmented cell, in a plane parallel to the epidermis. These cells

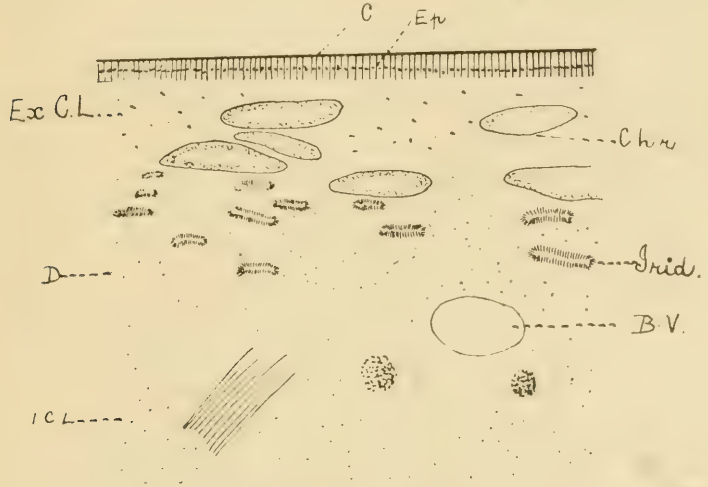

Fig. II.—Section of the skin. Highly magnified.

finally become differentiated into triangular muscular bands of fibrous tissue, the basal side of the triangle adhering to the wall of the vesicle, and the long thin apical region being lost amid the surrounding tissue of the dermis. A basal nucleus shows in each fibre.

3. The elasticity of the vesicle wall opposes the contractile tendency of the radial fibres. When the latter contract, and the wall relaxes, the vesicle becomes stretched out and flattened in a plane parallel to the

epidermis. When the chromatophores are thus expanded, the colour of the animal is very deep—this occurs when Eledone is excited in some way. When the radial muscles relax, the chromatophore contracts and the animal becomes pale, as when frightened. In the normally quiet state the chromatophore is in a state of tension, and is shaped like a biconvex disc (II, *Chr.*). In this stage it is in a semi-expanded condition, the contractile tendency of the two elements being equally balanced. However, the cell is constantly varying slightly in shape, as one or the other of the forces gets the upper hand; and so the chromatophore exhibits incessant slight tremulous movements. Hence when watching Eledone in an aquarium, one is struck by the constantly varying colour of the skin.

Harting, Blanchard and Girod agree that the vesicle is of ectodermal, and the girdle of mesodermal origin, but they consider that all motion on the part of the chromatophore is due to the amoeboid movements of the vesicle itself, while the radial fibres are connective tissue only.

Again Chun, who worked on the chromatophores of *Bolitaena*, a deep sea form, disagrees with both these views. In *Bolitaena* the chromatophore arises as a single ectodermal cell which sinks down into the dermis. The nucleus now divides repeatedly, while the cell throws out about 18 pseudopodial processes, in the equatorial plane parallel to the epidermis. At the base of each process is found a corresponding nucleus, which has originated as above. Later it is found that this girdle of processes has become differentiated into a ring of triangular muscular strands, whose contraction serves to expand the chromatophore. A second muscular region becomes differentiated round the periphery of the cell, and this opposes the radial tracks, tending to contract the

chromatophore. Hence Chun in *Bolitaena* derives the vesicle and the contractile apparatus wholly from one ectodermal cell. He has also traced the nerve supply of the chromatophores. For instance, the pallial nerve has several purely chromato-motor strands which run outwards to the external epithelium of the mantle, and there divide up ultimately into fine terminal nerves, one of which supplies each radial muscular strand, entering it at the narrow distal end. These nerves control the movements of the chromatophores, and therefore if the pallial nerve be severed the movements of the chromatophores on the corresponding side of the mantle cease. This method of origin, which Chun has described, may be peculiar to the chromatophores of *Bolitaena*, and is difficult to reconcile with the account given by Rabl and others.

In Eledone the pigment granules are very minute and of a reddish-buff colour. As in all Cephalopods, the motion of the chromatophores continues some time after death.

Iridocysts.—These are light-reflecting cells embedded in the dermis below the chromatophore layer. They are uninucleate flattened cells, each of which contains two rows of thin fibrillar laminae arranged parallel to one another and reflecting the light, and so giving rise to the peculiar metallic iridescence noticed in the integument.

II.—External Organisation.

The body may be divided into two regions—an anterior *cephalopedal mass*, and a posterior mass, or *visceral dome*, covered by the mantle.

As in other Octopoda these two regions are united dorsally by a thin superficial sheet of muscles. Externally the two regions of the body cannot be

definitely marked off, but merge gradually into one another. When touched with the hand, the body feels soft and slimy and of about the consistency of a firm jelly. The flesh retains its elasticity for some hours after death. The following are the dimensions of a probably full-grown Eledone, immediately after death:—

Length of arm	360 mm.
Length of visceral dome	160 mm.
Length of head	38 mm.
Total length	558 mm.
Width of head	75 mm.
Width of body at widest part ...	140 mm.

(A) **Cephalopedal Mass.**—This mass, which forms the greater part of the body of Eledone, as regards length, consists, as the name implies, of the head and foot.

(1) **Head.**—The head is a solid oval mass, behind the arms and anterior to the visceral dome. The anterior part or buccal mass is hidden away inside the bases of the arms, and hence only the posterior portion shows externally. Laterally it bears the eyes, while the central portion consists of the muscles which cover the brain cartilage, ventrally and dorsally. To the ventral surface of the head is attached the funnel (Pl. III, fig. 11, *F.*).

Cephalic Cartilage.—It is convenient to describe the structure of the Cephalic and Orbital Cartilage here. They are both built up of oval cells surrounded by a clear matrix (Pl. VI, fig. 66*a*, *C. cell* and *Matr.*). These cells have large oval nuclei, and are connected by fine cytoplasmic processes one with another. Hence the spaces occupied by the cartilage cells also intercommunicate by canals down which these cell processes run.

(2) **The Foot** is divided into eight equal muscular processes, or arms. In the female these are all similar, but in the male the third right arm is hectocotylised

counting ventrally from the dorsal surface. The arms are long, flexible tapering cones, slightly compressed laterally, and closely connected at their bases, to form a circular circumoral crown round the Buccal Mass (Pl. I, fig. 1, *Br. app.*). The bases of the arms are connected by a membranous semi-transparent web which extends for about one-fifth of the length of the arm, as an inter-brachial membrane. Further along it is continued as lateral wings—one on each side of each arm—which gradually diminish in size, and towards the distal end of the arm can no longer be distinguished (Pl. I, fig. 1, *W.*). This web is characteristic of the family Octopodidae, to which Octopus and Eledone both belong. Measuring the two dorsal arms and the body of half a dozen specimens of Eledone, it is found that the relative length of the arm, to the head and body, is 229 mm. to 113 mm. or roughly 2 to 1. There are about eighty suckers on each arm, arranged in a single row. They have no horny ring, and thus differ from the suckers in the Decapoda. Also they are much shallower, and none are modified into hooks. The suckers in Eledone are sessile, but the surface of the arm which supports them is raised up beneath each sucker into a flexible cylinder which really acts as a stalk, and allows it to move freely about. Successive suckers are separated from one another by a slight space. It is noticeable that when these suckers are applied to any surface, they do not keep in one straight row, but become displaced laterally so as to give the effect of several irregular rows of suckers on the arm. The sucker nearest to the mouth is about 3 mm. in diameter in a large specimen, and equals in size those about half-way down the arm. At first they increase in size working from the mouth towards the tip of the arm, and the fifth and sixth suckers are the largest which occur—about 12 mm. to

18 mm. in diameter. From here they steadily decrease again, towards the tip becoming almost too small for the naked eye to distinguish. The pressure they exert is very great, and must render the prey completely helpless. Even when only clinging to the hand with one tentacle, Eledone can hold on firmly enough by sucker action to enable one to lift the creature bodily out of the water. Frequently the skin is shed from the surface of application of the sucker.

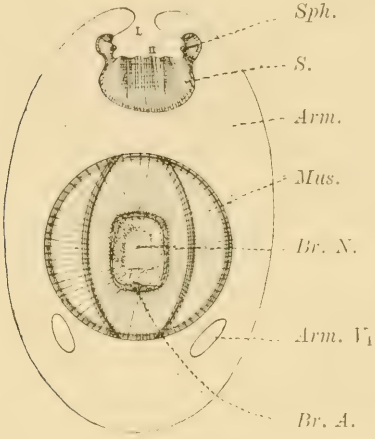

Fig. III*a*.

Fig. III*b*.

Fig. III (*a*) Trans. sect. distal part of arm showing relation of sucker (*S*).

Fig. III (*b*) Sagittal sect. of sucker of *Argonauta*.

Text fig. III *a*, shows a diagram of a transverse section through the arm, indicating the relation of the sucker to the remaining muscles. III *b*, is a modification of Niemiec's figure of the sucker of *Argonauta*. The outer surface of the sucker is covered by the general skin of the arm. The inner lining is a much folded epithelium, which covers the inner and outer divisions of the adhesive cup (III *a*, II and I). A sphincter muscle (*Sph.*) tends to close the upper and lower cups off from one another, and this muscle is opposed by the vertical extensor muscle (III *b*, *ext.*). When the sucker is applied

to any object, the extensor relaxes, the sphincter contracts, and the massive muscular base of the inner chamber is elevated to meet the sphincter. Thus we have a shallow flattened disc-like surface pressed closely against the object to be held. Now the extensor contracts and the sphincter relaxes a little, and the floor of the inner chamber is drawn away from the object, producing the desired vacuum.

All Cephalopods have power to regenerate injured arms. Frequently specimens of Eledone have been seen with several arms in process of regeneration. When an arm is first injured, it is curled up spirally towards the mouth so as to protect the injured part.

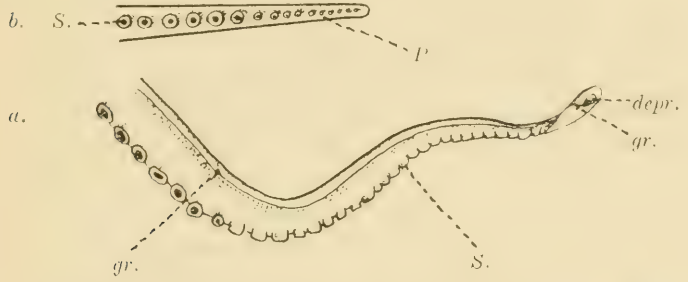

Fig. IV.—(*a*) Hectocotylised arm and (*b*) ordinary arm of male *E. aldrovandi*. x 2.

Hectocotylisation.—The third right arm of the male Eledone is hectocotylised, i.e., it is modified for the purpose of transferring the spermatophores expelled from the anterior opening of the funnel into the oviduct of the female. As no male *E. cirrosa* could be obtained, Text fig. IV *a*, shows the hectocotylised arm of a young male *E. aldrovandi*, which is very similar. Some Cephalopods have an autotomous hectocotylised arm, e.g. *Argonauta* and *Tremoctopus*, and in these hectocotylisation reaches its extreme state of specialisation. Spermatophores having been expelled from the funnel of

the male, are stored in this arm, which, when packed with them, becomes detached and in some way enters the mantle cavity of the female. The arm of Eledone, however, is less specialised and not autotomous, and the chief modification is at the tip, as in *Octopus*. Probably then the tip of this arm is inserted in the terminal part of the oviduct of the female, after the manner actually watched and figured by Racovitza in the case of Octopus. The hectocotylised arm of Eledone is somewhat shorter than the others—about 13 mm. less in the small specimen examined of *E. aldrovandi*. Examining the ventral surface, it may be seen that the third right arm—counting ventrally from the dorsal pair—bears a groove on its ventral aspect (IV, *gr.*). This is formed by a narrow fold of skin, and runs from the base to the tip of the arm, where the groove is enlarged to form an oval depression on the oral surface of the arm tip (IV, *depr.*). Moreover, the other seven arms of the genus Eledone are somewhat modified in the male. The suckers at the tip are set more closely together than in the female, and are shallower (IV *b*, *S*). The sixth and seventh suckers from the tip have practically no cavity at all, and the remaining ones are represented by tiny flat pads (IV *b*, *P*).

(B) **Visceral dome.**—This is the name given to the mass formed by the principal viscera of the body. Externally it is enclosed by the thick muscular mantle. It is oval in shape, being longer than it is broad, and bluntly rounded posteriorly. Anteriorly the visceral dome is marked off from the head by a slight constriction or neck. The dorsal surface is more convex than the ventral, and lies uppermost during creeping and swimming. As the shell is greatly reduced in Eledone, the visceral dome is unprotected save by the skin and muscular mantle.

Mantle.

The mantle encloses the visceral mass, forming a sac with thick muscular walls, which extends from the posterior end of the body as far as the posterior border of the head dorsally and of the funnel ventrally (Pl. I, fig. 1; Pl. II, fig. 8; M_1). Morphologically it is an outgrowth of the posterior part of the visceral envelope, and hence its inner wall is continuous with the outer wall of the visceral sac. The space between these two walls is the mantle cavity. The anterior edge of this sac is fused with the head dorsally, but ventrally and laterally it is free, so that a wide entrance to the mantle cavity is thus left.

The Mantle Cavity may best be studied by cutting the mantle down from the free edge on each side of the mid ventral line, so as to expose the organs contained therein. It is a deep cavity, as in Sepia and most Cephalopods, and is more spacious ventrally and laterally than dorsally, in order to enclose the important pallial complex. The body is bound to the enveloping mantle by:—(1) The above-mentioned dorsal fusion of head and mantle; (2) the shallow siphono-pallial articulation; (3) a vertical muscular septum running out from the median ventral line of the inner surface of the mantle to the visceral mass and dividing the mantle cavity into symmetrical halves; (4) the posterior continuity of the inner surface of the mantle with the external epithelium of the visceral mass; (5) two pairs of muscular bands running out from the afferent and efferent axes respectively of the gills—the band running along the outer surface of the efferent vessel is inserted on the inner ventral surface of the mantle, posterior to the insertion of the vertical septum, and that running along the inner

edge of the afferent vessel is inserted on the upper end of the mantle cartilage, near the insertion of the funnel retractor; (6) the depressor muscle of the funnel, running out from the funnel to the mantle, near the branchial heart (fig. 8, *F.D.*); and (7) the great lateral muscle running out from the cephalopedal mass to the mantle (fig. 8, *L.M.*).

The epithelium lining the mantle cavity is the internal continuation, over the free border of the mantle, of the outer skin of this structure, which here becomes much thinner and loses its chromatophores, and hence is transparent and colourless. However, the epithelium covering the dorsal side of the visceral sac bears large chromatophores, which show through the mantle during life on account of the transparency of this structure.

Stylets.—On removing the genital gland and the posterior portion of the alimentary canal, the dorsal portion of the mantle is exposed, internally. Two curved tracks can be seen, roughly forming a **V**-shape, posterior to the depressors of the funnel (Pl. III, fig. 13). By dissecting away these muscles, and the great lateral muscles, just at their bases, and then removing the inner epithelium of the mantle, two colourless, semi-transparent rods are exposed (Pl. III, fig. 13, *C.S.*). These are chitinous rods, oval in section and tapering at both ends, which reach down almost to the posterior end of the mantle, and are embedded in its substance (Pl. III, fig. 16, *a* and *b*). At the point of insertion of the funnel depressor the rods are thickest. Pl. III, fig. 15, represents a transverse section through the stylet, *in situ* in the mantle. Each stylet is enclosed in and secreted by the walls of an epithelial sac, one cell thick only. These cells are columnar, and are rather longer at the two ends of the sac than in the central region (fig. 15, *Ep.S.*). This

figure also shows that the rods are built up of concentric layers of chitin, the innermost, and therefore oldest, layers staining most deeply. Among the chitinous layers may be noticed a few cells with deeply staining nuclei. These are probably degenerate cells from the epithelial sac, which have become surrounded by chitin. Round the sac is a layer of connective tissue, outside which can be seen the muscles of the mantle (fig. 15, $M_1M.$). According to Appellöf, the epithelial sacs in Octopus, and therefore probably in Eledone, are formed by the shell gland. This gland, after closing and sinking below the external surface of the mantle, divides into two halves, each of which takes up a lateral position and secretes the stylet of its side. Hence these stylets represent the shell in Eledone, i.e., they are the homologues of the shell of other Mollusca, although much reduced in size and importance. The fact that the great muscles of the funnel, cephalopedal mass, and the muscles of the mantle radiate from these stylets, also gives support to this view. Possibly this degeneration of the shell in Eledone, as in other Octopoda, may be explained by the fact that it is no longer needed as a means of protection. For we must recognise that the means of offence and defence that Eledone still has are most efficient—powerful suckers, great biting jaws, immense bodily strength, together with the ink sac and large far-seeing eyes.

Dorsal fusion of head and mantle.—In the Decapoda the head and visceral dome are not as a general rule united dorsally. However, in Sepiola there is a narrow connection between the two. Eledone, like Octopus, shows this dorsal fusion in a more complete stage. A thin sheet of muscle is continued anteriorly from the dorsal edge of the mantle over the region of the eyes, and fuses with the muscular bases of the arms, thus forming a firm dorsal union between the head and visceral dome.

Siphono-pallial articulation.—This is very weak in Eledone, as in all Octopoda. It consists of two shallow ridges on the postero-ventral edge of the funnel, which fit in two corresponding shallow grooves of the anterior and inner ventral surface of the mantle (Pl. II, fig. 9*a*, *l.f.r.*, *l.m.gr.*).

Vertical muscular septum.—This consists of two symmetrical triangular sheets of muscle, which run out from the mantle to the body and enclose the anus between their anterior edges (Pl. II, fig. 8; Pl. III, fig. 11, *m.s.*, $m_1 s_1$ and *an.*). The septum is covered by the general epithelium of the mantle cavity. The shortest side of each sheet is anterior, while the longest runs from the base of the mantle out obliquely to the visceral mass. The vertical line of attachment of the septum extends from the ventral posterior extremity of the mantle to within half an inch of its anterior edge (figs. 8 and 11, *m.s.a.*). By referring to fig. 11 it will be seen that after the septum enters the mantle cavity (*e.m.*), it is free for some distance from the visceral mass, and hence adheres only to the mantle. About half-way up the length of the oviduct, it becomes attached to the visceral mass. Hence there is free communication, posteriorly, between the right and left halves of the mantle cavity (fig 11, *P.C.*). Each of the two halves of the septum consists of two rather thin sheets of muscle—(1) an upper sheet sloping from the mantle, obliquely inwards and downwards, to the body (figs. 8 and 11, m_1); and (2) a lower sheet sloping from the mantle, obliquely inwards and upwards, to the body (figs. 8 and 11, *m.p.*).

The lower strands of the upper sheet and the outer strands of the lower sheet run towards one another, and form a superficial sheet which runs along with the funnel retractor muscle, down to the mantle (fig. 11, *m.l.*,

m.p. ex., *F.D.*). The upper strands of the upper sheet, and the inner strands of the lower sheet, after a superficial course run together, and sinking deeper join in with the great lateral muscle.

Muscles attaching gills to mantle.—The narrow muscular band which runs along the external surface of the efferent vessel of the gill, from the tip downwards, after leaving this artery at the base of the gill, runs obliquely inwards over the ventral surface of the kidney to meet its fellow in the middle line (Pl. V, fig. 37, *Br.M.*). The common strand now runs posteriorly, over the ventral surface of the genital capsule, and is inserted on the inner face of the mantle, just posterior to the vertical septum. Possibly this strand affords additional support to the genital gland, when it is enlarged at the time of sexual activity, as well as serving to deflect the gill.

Funnel.

This may well be studied along with the mantle cavity, as it is closely related thereto. It is a hollow conical structure, truncated anteriorly (Pl. II, fig. 8, *F.*), which is attached to the ventral surface of the head, and is free laterally and ventrally, and for about the anterior third of its dorsal wall (fig. 11, *F.*). The anterior and external opening of the funnel is about 13 mm. in diameter, in a large specimen, while the posterior internal opening is very much larger and forms the base of the cone. At the posterior end, the ventral edge of the funnel is recurved, ventrally and anteriorly. This forms a ridge, which is more pronounced at the sides than in the centre, and forms part of the funnel articulation (Pl. II, fig. 9*a*, *l.f.r.*). The weak locking apparatus is in strong contrast with the firm one found in *Sepia*, *Loligo* and

other Decapods, and this means of locking the mantle seems to have weakened as the dorsal fusion formed, and so rendered it less necessary. Also, as Eledone is a much less powerful swimmer than the Decapods, the need of a strong funnel articulation is lessened. The funnel cavity is three-chambered. The central largest chamber alone opens to the exterior, while the lateral chambers are blind anteriorly. All three, however, open into the mantle cavity. The central chamber is cut off laterally from the side chambers by the great depressor or retractor muscle of the funnel. This forms the ventral and ventro-lateral wall of its own side of the funnel, and then runs out to its insertion on the anterior border of the mantle cartilage of its side. Two other pairs of muscular bands, which are narrow and rather short, run in from the dorsal surface of the funnel to the cephalopedal mass. They act as protractors of the funnel, and are exposed by cutting through the skin behind the funnel, as in Pl. II, fig. 9, *sk.*, and turning the funnel ventrally. The protractors form a letter **W**, the external pair being inserted above the inner pair, on the funnel wall. The external pair run outwards and dorsally, to join in with the capito-pedal muscles just below the eyes. The internal pair run inwards to the ventral surface of the cranial cartilage, and are attached there. The dorsal wall of the funnel is formed by a broad pair of muscles which then run outwards from the posterior lateral region of the funnel to the top of the mantle. Thus with the depressor, these two nuchal or collar muscles bound the lateral funnel chamber. Hence the funnel muscles are arranged in three sets:

(*a*) One pair of depressors (fig. 9*a*,, *F.D.*),

(*b*) One pair of nuchal muscles (fig. 9, *coll.*), and

(*c*) Two pairs of protractors (fig. 9, *L.F.Pr.*, *L.F.Pr*$_1$).

From the above description it can be seen that, although water may enter the mantle cavity all along the external opening of the mantle, yet when the funnel is locked the only way out for the contents of the mantle cavity—excretory or genital products, water, &c.—is through the central funnel chamber. As in other Octopods, Eledone has no valve in the funnel. It has, however, a large and elaborate mucous gland—Müller's gland (Pl. II, fig. 10, *f.o.*). This is four-lobed, and is an elaboration of the internal epithelium of the funnel, and may best be seen by opening the funnel ventrally, as in Pl. II, fig. 15. It serves to lubricate the internal surface of the funnel, which consequently is generally coated over with opaline viscous mucus, rendering the gland itself rather obscure in fresh specimens. It may be seen, however, on scraping the mucus away.

Pallial Complex (figs. 8 and 11).—Under this general term may be included those important organs situated in the mantle cavity, together with the external apertures of certain internal organs. Eledone, like other Cephalopods, in spite of its high specialisation along certain lines, has yet retained its primitive symmetry in certain features, including the pallial complex. The organs of the pallial complex are:—

(1) A pair of **Gills**, one on each side of the visceral mass, and attached to it by muscles, vessels, &c. (fig. 11, *g.*);

(2) The **Anus**, situated anteriorly, between the left and right halves of the vertical septum (fig. 11, *an.*);

(3) The **Urinary papillae**—one pair, protruding for about 12 mm. in a large specimen into the mantle cavity, just in the angle between the base of the gill and the visceral mass (fig. 11, *Ur. p.*). The urinary aperture is a small hole at the tip of this papilla;

(4) **Genital ducts.** In the female these are a pair of equally developed oviducts, which may be seen running below the visceral epithelium from the urinary papilla upwards for 12 to 24 mm., according to the size of the specimen. The tip of the oviduct is alone free, and protrudes for a short distance out from the visceral mass into the mantle cavity, bearing the oviducal aperture at its end, somewhat below the anterior end of the gill (fig. 11, *od. ap.*). In the male (fig. 8), there is a single genital duct—the penis—situated similarly to the left oviduct in the female (*pen.*).

Other organs exposed on opening the mantle cavity. - After removing the vertical septum the following are seen :—

(1) The intestine, running vertically up in the median line, over the liver to the anus, with the anterior vena cava lying on its left side;

(2) The ventral surface of the liver, covered by the visceral envelope; and

(3) The two kidney sacs, posterior to the liver.

Visceral envelope.—On removing the epithelium and the septal muscle, which envelop the visceral mass of Eledone, a muscular envelope external to this visceral mass is exposed. Over it ventrally run the visceral nerves (Pl. IX, fig. 69, *Visc.N.*). This envelope, dorsally, runs from the posterior border of the cerebral cartilage, to which it is attached, down to the level of the branchial hearts, where it becomes adherent to the muscular mantle. The dorsal region of the envelope is stouter than the ventral, and contains large widely separated chromatophores, which probably show through the mantle during life. The thin ventral region covers over the liver and ink sac, but is dorsal to the rectum. It runs back from the ventral posterior edge of the cranial cartilage to the

anterior edge of the posterior division of the great venous sinus (Pl. VII, fig. 53, S_3V_3), to the wall of which it is attached by connective tissue. Ventrolaterally the envelope is reinforced by the depressor muscles of the funnel. Dorsolaterally it is similarly strengthened by the great lateral cephalopedal muscles.

General conclusions.—Considering Eledone as a type of the Cephalopod organisation, the following characters are noticed:—

1. It retains the primitive bilateral symmetry of the Phylum, and hence in this respect is less specialised than many Gastropods such as Helix.

2. On comparison with more primitive members of the Phylum, e.g. Chiton, it is seen that profound changes have evidently occurred in the inter-relations of the head, foot and visceral dome. The alimentary canal has turned forward posteriorly, so becoming **U**-shaped. The anus has been ventrally approximated to the mouth, the free ends of the gills point anteriorly, the true morphologically ventral surface of the body has been greatly abbreviated, and the dorsal correspondingly lengthened. The mantle now has the form of a pouch or sac, enclosing the visceral dome. Simultaneously with these changes the foot ceased to be used merely as a ventral creeping organ, and was transformed into a circumoral mass. Probably this was effected by the lateral regions of the foot growing up dorsally, on each side of the head, and finally fusing above it, the anterior edge meanwhile growing out into long flexible processes.

DIGESTIVE SYSTEM.

The following is the best method of dissecting out the alimentary canal:—

1. Remove the funnel from the ventral surface of the head.

2. Cut down the web between the two ventral arms, beginning anteriorly, and continue the cut down along the ventral surface of the head, thus exposing the Buccal bulb and the cartilage surrounding the brain.

3. Loosen the intestine from the liver, dissecting out the ink sac from its place on the latter, so as to enable the intestine to be turned back.

4. Loosen the liver at the sides, where it is connected to the cephalopedal muscles, by cutting through the visceral envelope, and then turn the liver forwards (Pl. V, fig. 38*a*). The organs enclosed in the visceral sac are now exposed. Pl. IV, fig. 17, represents the alimentary canal, entirely dissected away from the surrounding tissues, to give a clear representation of the relations of the various parts. The alimentary canal is essentially a **U**-shaped tube, the ventral limb of the **U** being the shorter, and the anus being approximated to the mouth.

The Mouth is situated in the centre of the oral and anterior surface of the arms (Pl. II, fig. 5). It is circular, about 12 mm. to 22 mm. in diameter in large specimens, and is surrounded by a circular lip the edge of which is furnished with short finger-like papillae (Pl. IV, fig. 17, *m.*; Pl. II, fig. 6, *l.*). The external surface of the lip is continuous with that of the web, and only marked off from it by a deep groove (fig. 6, gr_1). This edge of the web forms a kind of contractile outer lip. The mouth leads into a cavity with very thick and muscular walls. This is the **Pharynx** and the oval

muscular mass enclosing it is known as the **Buccal Mass** (fig. 17, *B.M.*). The buccal mass is surrounded, and therefore concealed, by the muscular bases of the arms (Pl. III, fig. 14, *B.M.*, *arm*). The pharynx is furnished with two powerful chitinous jaws, whose shape curiously resembles that of a parrot's beak, and which are placed dorsally and ventrally. Unlike the parrot, however, the ventral jaw of Eledone, which bites outside the dorsal, is the larger and wider (Pl. IV, fig. 27, J_1 and J.). These jaws bite vertically with great force, tearing up the food captured and held by the suckers before it is passed on to the rasping action of the radula. The anterior edge of each jaw is thick, and dark brown in colour. The trenchant border is sharp, and a raised ridge some distance behind this gives attachment to the muscles working the jaws (fig. 27, *r.*). This part of the jaw is exposed by cutting away the lip (Pl. IV, fig. 24). Further in, they decrease in thickness, and their colour lightens, and posteriorly they are thin, colourless, and semi-transparent. On the floor of the pharynx, slightly anterior to the middle point, is a muscular outgrowth—the tongue (fig. 24, *t.*). This forms the anterior wall of the Radula sac, at the base of which is the growing point of the radula (fig. 24, *rad.*). The Radula is a broad chitinous ribbon which, issuing out of its sac, runs over the upper and anterior surface of the tongue, which is responsible for the rasping action of the radula, as it works forwards, backwards and laterally. The tongue is strengthened internally by two small cartilaginous strips, which give it rigidity and also provide attachment for its motor muscles. Here, then, the food cut up by the jaws is further triturated. The teeth of the radula are large, and each row consists of three on each side of a central large tooth. The innermost of the three is the smallest,

and the outermost has a broad basal attaching portion (Pl. IV, fig. 25, *Cc.*, 1, 2 and 3). The radula, when removed from its sac, is about 50 mm. long. In front of the tongue is another outgrowth, the Sub-Radular organ, on the tip of which opens the duct from the posterior salivary glands. Thus the secretion from these glands is poured on to the food before it is acted on by the radula (fig. 24, *s.r.o.*, $s_1 g_1 d_1$). This duct enters the buccal mass below the radular sac, after running above the sub-lingual gland which is on the ventral surface of the bulb (fig. 24, *s.l.g.*). The paired ducts from the anterior salivary glands open into the pharynx laterally and posteriorly (fig. 24, *s.g.d.*). Thus it will be seen that the massive muscular wall of the buccal bulb is formed chiefly by the muscles working the jaws and the radula. Anteriorly it is attached to the bases of the arms by a circular muscle band (Pl. III, fig. 14, and Pl. IV, fig. 20, *circ. m.*), and posteriorly by two ligaments (Pl. VII, fig. 53). Posteriorly the pharynx is continued into the oesophagus.

The Oesophagus is a narrow tube running down posteriorly to the stomach (fig. 17, *oes.*), dorsal to the hepatic gland (Pl. V, fig. 38*a*). Its posterior end marks the limit of the stomodaeum, the stomach, spiral caecum and intestine being hypoblastic in origin in all Cephalopods, while that part of the rectum posterior to the aperture of the ink duct represents the very small proctodaeum (Korschelt and Heider).

The internal surface of the oesophageal wall is thrown into numerous longitudinal ridges (Pl. IV, fig. 18, and Pl. V, fig. 33). Internally it is coated by a thin chitinous layer, ridged correspondingly, which is continued posteriorly as the chitinous lining of the stomach (fig. 33, *Cut. L.*). About half-way down, the oesophagus bears a large pouch-like non-glandular

dilation or crop. This is also lined with chitin, and folded, and serves as a food reservoir when the stomach is full (fig. 18, *cr.*). At the base the oesophagus dilates, and its wall and chitinous lining become smooth. (To expose the anterior part of the oesophagus it will be necessary to remove the ventral wall of the cranial cartilage and the sub-oesophageal ganglia.)

Salivary Glands.—Eledone has five salivary glands:

1. Anterior salivary glands, 1 pair, closely applied to the external surface of the buccal mass, posteriorly (fig. 17, *r.s.g.*).

2. Posterior salivary glands, 1 pair, situated at the side of the crop (fig. 17, $r.s_1\ g_1$, and fig. 38*a*, $s_1\ g_1$).

3. One sub-lingual and median salivary gland, situated in the ventral wall of the buccal mass (fig. 24, *s.l.g.*).

These glands are granular in appearance, soft and spongy in texture, and of a translucent whitish colour. The anterior pair is much smaller than the posterior, and is attached in the angle between the oesophagus and buccal mass (Pl. IV, fig. 20, *s.g.*). They are flattened oval glands, bilobed posteriorly, and are about 16×12 mm. in large specimens. The duct leads from a slightly elevated ridge on the internal surface, inwards to the pharynx, and is very short. Along with the duct, the artery and nerve of the gland enter by this ridge (Pl. IV, fig. 22).

The posterior glands are large and flattened, and the crop must be turned aside to expose them fully. They are attached to the visceral sac by a suspensory ligament. The duct leaves the anterior internal region where there is a slight depression. Here also enters the artery of the gland (Pl. IV, fig. 21, $s_1\ g_1\ d_1$). They measure about 32 mm. × 25 mm., and the duct after a short course joins its fellow to form an unpaired median "posterior salivary

duct," which runs forward alongside the oesophagus to the buccal mass (fig. 17).

The sub-lingual gland is oval, and thickened posteriorly (Pl. IV, fig. 23, *s.l.g.*). In those Cephalopods whose development has been studied, it arises as an infolding of the ventral wall of the pharynx of the embryo, below and anterior to the sub-radular organ. This infolded region then gives rise to many tubular caeca, each of which opens independently by a minute opening into the buccal cavity. These tubules, connected together by indifferent tissue, thus form the compact sub-lingual gland. The three salivary glands all consist of glandular secretory tubules, embedded in a stroma of connective tissue (Pl. V, figs. 34 and 35, *Tu.*, *Str.*). These tubules are closely adpressed in the anterior glands, but much further apart in the posterior glands, and branch dichotomously here (figs. 35 and 34). The secretory cells of the three glands are all similar, and are columnar with a basal nucleus. The secretion forms in globules in the anterior portion of the cell, and then falls into the lumen of the tubule (Pl. V, fig. 36). The secretion of these glands is a kind of mucus only, and contains no ferment whatever (Frédéricq and Bourquelot). The venous blood, collecting in the sinuses occurring in the stroma of connective tissue which binds the secretory tubules together, passes out directly into the perivisceral venous sinus.

Stomach.—This is a very muscular grinding organ, reminding one of the gizzard of a bird. Its ventral and dorsal walls are thickened anteriorly into grinding pads. These are thick and stout, and ridged internally. The posterior and lateral walls are, however, thinner. The oesophagus opens into the stomach at its right anterior angle, and the origin of the spiral caecum and intestine

is quite near this point (figs. 17 and 18). In size the stomach is rather less than the crop, and like the oesophagus is lined by an easily detachable layer of chitin. This lining is specially thick where it covers the grinding pads (figs. 18 and 19, ch_1, *pad.*). Where it covers the posterior wall of the stomach, however, it is smooth and thin. At the exit of the spiral caecum and intestine the cuticle ends, thus leaving a circular orifice through which food passes onwards from the stomach (Pl. V, fig. 38, *or.*). The food is ground in the stomach, and also well mixed up with the digestive fluid which enters from the spiral caecum (Bourquelot), so that here digestion takes place.

Spiral Caecum.—A narrow passage leading out from the stomach, soon bifurcates, and so gives rise to the spiral caecum on the one hand and the intestine on the other (Pl. V, fig. 38, *Int. ap.*).

The spiral caecum is in reality a long narrow sac, e.g., caecum in *Loligo*, which in the Octopodidae and others becomes curled in a spiral of one and a half turns. It is thin walled, and the internal septa are seen faintly from outside (Pl. IV, fig. 28). The columella of the spiral is on the side opposite to the intestine (fig. 38). On cutting open the caecum along the columellar edge, and pinning it out, it will be seen that there is a series of delicate folded valves, running transversely to its length (fig. 38, *v.*, v_1). Cuvier described a spiral valve running down the caecum in Octopus, but in Eledone there is a series of short transverse valves instead, closely set. They are widest centrally, and taper at their two ends, which are attached to the columellar region of the wall. Along this columellar region also runs a longitudinal fold, at the side of which enters the common hepatic duct, some distance from the anterior end of the caecum (fig. 38, *h. ap.*). Probably this fold guides the digestive secretion

into the stomach and also into the intestine. Like the intestine, the inner wall of the caecum is not covered by any chitinous lining. It acts as a reservoir simply for the hepato-pancreatic secretion, and no food of any kind was recognised therein.

The Intestine.—Leaving the stomach, this long, thin-walled, and slender organ, after running between the two hepatic ducts, before their fusion, curves ventrally upwards over the liver, over the ventral surface of which it runs, curving first to the right, then in again to the left, and then anteriorly to the anus. Just before it reaches the anus, the ink duct enters the rectum by an aperture at the tip of a small papilla on its dorsal wall. The anus has a dorsal and a ventral lip, and bears two small leaf-shaped appendages or " ears " laterally (Pl. IV, fig. 29). The internal wall of the intestine is ridged, the two most prominent ridges being continued up from the columellar ridge of the spiral caecum. In the initial part of the intestine, the food which has been in great part digested in the stomach is mixed with that portion of the hepato-pancreatic fluid which enters this organ. Hence digestion is completed here. The chief process, however, occurring in the intestine is absorption of the now digested food. Towards the rectal end of the intestine, waste matter of a dull orange tinge collects.

Digestive Gland.—This large oval gland, although often called the liver, does not secrete a fluid at all comparable to the bile secreted by the liver of vertebrates. It occupies almost the whole of the visceral sac, and lies ventral to the crop and oesophagus. Although in Eledone it consists of one lobe only, the paired ducts and the analogy with the Decapods indicate a fusion of two originally distinct glands, which were situated laterally to the gut. The ink sac lies in a deep groove excavated on the ventral

surface of the liver (fig. 17), and the two organs are surrounded by a common iridescent membranous envelope, outside and in addition to their individual coverings. In a freshly obtained Eledone a bilobed oval whitish region can be distinguished round the origin of the two hepatic ducts (Pl. VIII, fig. 32, *P.*). This is the so-called pancreas, and shows up distinctly against the yellowish green liver. The digestive gland as a whole is soft and spongy, and enclosed in a very delicate membranous envelope. It is built up of branching secretory tubules which open into the hepatic ducts. The pancreatic tubules likewise open into these ducts, further down.

According to Bourquelot, the digestive hepato-pancreatic fluid poured into the spiral caecum is colourless before digestion, and brownish after it. The hepatic secretion consists of diastase, trypsin and pepsin, while the pancreas secretes diastase also.

The opaque rather thick-walled hepatic ducts run posteriorly, and after embracing the intestine unite to a common channel which enters into the spiral caecum (fig. 28). Hence the order of events in the digestive economy of Eledone is as follows:—

(1) Food seized by the suckers is torn up by the jaws and passed into the mouth.

(2) Here it is mixed with the mucous secretion of the sub-lingual and posterior salivary glands.

(3) Next the radula rasps it and further breaks it up.

(4) As it passes into the oesophagus the secretion of the anterior salivary glands is poured over it.

(5) Now it passes to the stomach. Here the food is ground and mixed well. The hepato-pancreatic ferments enter from the caecum or reservoir, and become mixed with the food, and so digestion takes place.

(6) Next the food passes on out of the stomach into

the intestine, being prevented from entering into the spiral caecum by the folds of the wall in this region.

(7) In the intestine digestion is finished, as some proportion of the digestive fluid enters here. This region is, however, chiefly that of absorption. After this, the waste matter passes up to the anus and is ejected.

The Ink Sac, or anal gland of Eledone is a long, somewhat pear-shaped gland, which opens into the dorsal wall of the rectum, on a slight papilla, very near the anus (Pl. IV, fig. 30, *I. p.*). It is a much less developed structure than the ink sac of the Decapoda, and, unlike the latter, lies embedded in a groove on the ventral surface of the liver, in a median position (Pl. VIII, fig. 32). To expose it, the visceral envelope, and then the common iridescent membrane round the liver and ink sac, must be removed. Its dorsal wall lies in close contact with the ventral epithelial wall of the liver. When the enveloping membranes have been removed, the ink sac shows as a dull metallic dark-blue organ. Great care must be taken not to cut the wall, for the thick viscous secretion is exceedingly hard to get rid of, and stains the dissection deeply. The nerves should be traced before removing the visceral envelope. They come from two sources in Sepia, and probably also in Eledone (Girod). However, only those from one source have been followed out, i.e.:—

(1) The visceral nerves running over the liver, in the neighbourhood of the ink sac, send several branches inwards, which end in its walls (Pl. VIII, fig. 31, $I_1 S_1 N_1$). Near the posterior end of the sac, a specially large nerve runs in from each visceral trunk, and this, after pursuing a downward course until it meets the artery and vein of the ink sac, enters the gland along with them (fig. 31, *I.S.N.*).

(2) In Sepia a branch from the gastric ganglion may be followed up the wall of the intestine to its tip. At the point where the ink duct joins the intestine this nerve gives off a very fine branch which runs down the wall of the duct and gland to the posterior end. This nerve regulates the secretion of pigment, while the visceral nerve branches control the muscular contraction of the ink sac (Girod).

The ink sac has rather an elaborate vascular system. The abdominal aorta, running up from the heart to the intestine, gives off a vessel to the ink sac (Pl. VI, fig. 49, *I.S.A.*). This enters at its base, first giving off at each side a spirally curved vessel to the corresponding lobe of the pancreas (fig. 32, *P. A.*). Then it divides into four vessels, which become embedded in the wall of the ink sac and send branches to the internal glandular trabeculae. The ink duct also receives a small artery from the terminal portion of the intestinal vessel.

The vein runs from the sac into the posterior part of the anterior vena cava (posterior hepatic vein). It is formed by the union of two vessels which run one on either side of the ink sac and unite at its base. On their way these receive branches from the sac, and much longer ones from the liver and pancreas (fig. 32, *I.S.V.*).

Structure.—Cutting a sagittal section of the gland, the following portions may be seen:—(1) The basal glandular part (Pl. IV, fig. 26, *I. gld.*); (2) the reservoir above this (fig. 26, *Res.*); and (3) the duct, of about equal length with the gland. Its terminal portion lies external to the visceral envelope (fig. 32), and bears two internal valves, just near the anterior end.

The glandular part, after being well washed, will be seen to consist of numerous trabeculae, which branch and run into one another (fig. 26, *tr.*). These are membranous,

perforated by small holes, and consist of a thin layer of connective tissue covered on either side by the secretory columnar epithelium. An oblique diaphragm limits the region of the gland, and is perforated by a hole for the passage of the ink. At the base of the gland is found a whitish mass of round non-glandular cells (fig. 26, gld_1). This is the formative region where the trabeculae originate. The initially indifferent cells become differentiated into either the connective tissue or the secretory cells of the trabeculae. These trabeculae are constantly being formed and travelling forwards to the anterior end of the glandular region. Tracing their course and structure as they go, it is found that the young cells gradually accumulate pigment granules, and when they are full burst. Thus the ink is freed and the secretory cells destroyed. Towards the anterior end of the gland, then, the trabeculae disintegrate, and are constantly replaced by the younger ones behind (Girod). The secretion is a thick dark-brown liquid, and a few drops will colour a large volume of water. On drying, a dark-brown powder is obtained. The liquid consists of a colourless transparent plasma, having minute dark-brown pigment granules in suspension. On analysis it is found to contain both copper and iron, extracted from the blood (Girod). Although the actual secretion of the ink is continuous, its passage to the exterior is intermittent and voluntary. After expulsion from the anus, the ink is discharged, along with a jet of water, through the funnel.

CIRCULATORY SYSTEM.

In order to dissect the vascular system of Eledone adequately, it is necessary to inject the vessels. The venous system is best injected from the anterior vena cava, and the arterial system from the base of the efferent blood vessel of one side. As the veins lie more superficially than do the arteries, it is best to follow them out first. If dissecting one specimen only for all the systems, only the main blood vessels, e.g., the anterior, abdominal, genital and efferent arteries, the three venae cavae, and the veins of the arms, can be followed satisfactorily.

The circulatory system will be described under the following headings:— (1) Blood, (2) Heart, (3) Arterial system, (4) Venous system.

The course which the blood follows in the body may be briefly summarised as follows:—Blood which has been aerated in the gills returns by means of the two efferent vessels to the auricles, and thence into the ventricle of the heart. From there it passes out to the body by the anterior, posterior and genital aortae, and ultimately reaches the arterial capillaries. Thence passing into the veins, it finally enters the lateral venae cavae, which take it back to the gill, thus completing the circulation.

Blood.

The blood of Eledone is a clear limpid fluid, of very pale blue colour. For examination it may be easily obtained by opening the efferent artery, at the base of the gill, or the anterior aorta, or again the anterior vena cava. In contact with the oxygen of the air the blue colour soon deepens. The various constituents of the blood are:—

(1) Small colourless amoeboid and very granular

corpuscles of 15 μ diameter (Pl. VI, fig. 44), with rounded or slightly curved nuclei. After a lapse of several minutes, these corpuscles are seen—if the blood is placed in a watch-glass after withdrawal from the body—to congregate together in large clusters.

(2) A liquid medium, in which the above corpuscles float, containing:—(1) Mineral salts (including iron in small quantity, Girod); (2) slight traces of organic compounds; and (3) 9 per cent. of the substance Haemocyanin, an albuminous compound containing copper. According to Cuénot, it is the great quantity of copper present which gives the blue tinge to the blood. This darkens when exposed to air, because of the oxidation of the copper. The blood of Eledone, like that of all Cephalopods, contains no fibrin. The analysis of the contents of the blood plasma has not been made for *E. cirrosa*, but Frédéricq and Cuénot made it for Octopus and Sepia respectively. Two glands have been suggested as the seat of origin of the blood corpuscles:— (1) The branchial gland (Joubin), and (2) the white body (Faussek).

Heart.

In Eledone the heart is situated just behind and to the right of the stomach (Pl. VI, fig. 42, *V.*). It is, however, rather ventral to this organ, but dorsal to, and therefore concealed by, the kidneys

The heart is rather smaller than the stomach, and consists of three chambers, two auricles and a central ventricle, into which the auricles open laterally, one at each side. The two auricles are essentially the dilated and slightly muscular basal portions of the efferent branchial vessels, and may be defined as the portion of these vessels lying between the posterior end of the gill and the ventricle (fig. 42, *au.*). The auricles are symmetrical, but the thicker walled, more fleshy ventricle

is asymmetrical in shape. The walls of this chamber are muscular and, unlike the dark coloured branchial hearts, of a whitish colour. The inner surface is produced into numerous branching and interlacing fleshy pillars, which are bathed in arterial blood (Pl. VI, fig. 45). The cavity of the ventricle is incompletely divided into two chambers by a fleshy partition which probably aids in ensuring the distribution of blood through all three aortae during the period of systole. This is triangular in shape, and as the dorsal and anterior edges are attached to the corresponding walls of the heart, while the basal side hangs free, an incomplete vertical septum is thus formed. (Pl. VI, figs. 47 *a* and *b*, *tr. s.*, and fig. 45). The right auricle leads into the right chamber, and the left auricle similarly into the left chamber of the ventricle. The anterior aorta is given off from the right anterior dorsal corner of the heart, while the abdominal aorta leads out of the ventral surface of the left chamber and the genital aorta from the posterior dorsal wall of the same (figs. 45, 46 and 47). Two semi-lunar valves guard the entrance of each auricle into the ventricle. The free edge of each is directed inwards into the ventricle (fig. 48, *au. v.* and $au_1\ v_1$). Consequently, at the moment of diastole they open and allow blood to enter the ventricle from the auricles, and at this time the blood in the two chambers of the ventricle can mix freely. However, at the moment of systole the valves close and prevent the reflux of blood into the auricles. The ventricle is now completely divided into two chambers by the partition, and the blood from the right chamber is forced up the anterior aorta, while the blood in the left flows into the abdominal and genital aortae. The anterior aorta also has two smaller semi-lunar valves at its base. These have their free edges turned towards the aorta. They close during diastole, and open during systole.

Arterial System.

The arterial blood in Eledone, as in Octopus, is wholly enclosed in definite vessels. These have muscular walls, which are consequently stronger and thicker than the membranous walls of the veins. The pressure of the blood in the arteries is very great indeed, but is slight in the veins (Frédéricq). As mentioned previously, the arteries of Eledone radiate from three main trunks:— (1) Anterior aorta, carrying blood to the cephalopedal mass, the mantle and anterior portion of the alimentary canal; (2) abdominal aorta, carrying blood to the intestine and ink sac; and (3) genital artery, running direct to the genital gland.

The anterior aorta is a large vessel which, leaving the heart, runs forwards, and curving round the liver runs dorsal to this organ, and then lying to the right of the stomach follows its outline for a time. Then, entering the large venous sinus surrounding the oesophagus, it runs alongside and to the right of the latter almost as far as the cranial cartilage (fig. 42, *Ant. A.*). Soon after its origin, the anterior aorta gives off a large branch which immediately bifurcates into the right and left pallial arteries (fig. 42, *L. Pall. A.*). The right vessel curves round dorsal to the aorta, and then runs internal to the visceral envelope, towards the funnel retractor. Just interior to this it gives off a vessel which runs up anteriorly, on the inner side of the visceral envelope, giving off several small branches during its course (fig. 42, $V_1E_1A_1$). This artery, after furnishing several small branches to the retractor infundibuli, ends in the base of the funnel. The main pallial vessel now runs below the posterior part of this funnel retractor muscle, and so gains the inner face of the ventral part of the mantle, and then runs obliquely to the stellate ganglion

(fig. 42, *St. G.*). On its way it gives off several branches to the right and left, which end in the substance of the mantle. Running below the stellate ganglion, the pallial artery ends in several branches which divide up in the mantle substance.

The left pallial artery runs just internal to the visceral envelope, dorsal to the stomach, where it gives off a posterior branch to the visceral envelope. Then, running almost transversely to the left, it gains the left depressor of the funnel, after giving off an anterior branch. From this point its course is similar to that of the right pallial artery (fig. 42, *L. Pall. A.*). Entering the venous sinus, the aorta gives off a second large branch, the visceral artery, which immediately gives off a branch ending in small arteries on the right side of the stomach. Next it gives off a large hepatic artery, which enters the liver dorsally and posteriorly, and breaks up in its substance (fig. 42, *Hep. A.*). Then, running down the groove between the oesophagus and the stomach, it gives an anterior branching artery to the lower part of the oesophagus (fig. 42), an artery to the left wall of the stomach, a branch to the intestine, and ends in many branches to the spiral caecum. The aorta is hidden anteriorly by the crop and salivary glands; when these are turned aside it may be seen to give off a branch at the level of the crop to the alimentary canal (fig. 42, *Oes. A.*), and this branch gives off an anterior and a posterior fork to the corresponding parts of the oesophagus, and several branches to the walls of the crop. Near the anterior end of the visceral envelope, the aorta gives off a small dorsal artery to the muscles of the neck (fig. 42, *N.A.*), and then divides into two smaller forks which run one on each side of the oesophagus. An aperture on the ventral surface of the brain, between the anterior infundibular nerves,

allows these two arteries to leave the central cavity of the brain, through which they pass posteriorly, and gain the ventral surface of the buccal mass, over which they run obliquely (fig. 42, *C.A.*). At the anterior end of this mass, each cephalic artery divides again. A second division of these four branches now gives the eight brachial arteries (fig. 42, *Arm. A.*) which supply the arms.

Each brachial artery runs down the centre of the arm, external and closely applied to the brachial nerve (Pl. VIII, fig. 80). Externally it gives off a series of small arteries all along the arm, to the muscles and skin of the external surface of the arm, and to the web (Pl. VIII, fig. 79). Internally the brachial artery furnishes two branches to each sucker (fig. 79, *S. a.*). These run up one on each side of the corresponding nerve ganglion, and penetrating the muscles of the arm, end in superficial small branches on the sucker and internal surface of the arm. The brachial artery extends to the tip of the arm, its size decreasing with the corresponding lessening of that organ towards the tip.

Although the anterior and posterior salivary glands are widely separated from one another, yet their arteries have a common origin. Soon after its bifurcation, the anterior aorta gives off two branches, one from each fork (fig. 42). Each branch immediately divides again, one artery running posteriorly to the corresponding posterior salivary gland, which it enters anteriorly (fig. 42, $S_1 A_1$), and one branch (the pharyngeal artery, fig. 42, *Ph. A.*) running anteriorly to the buccal mass.

The pharyngeal arteries run forwards, one on each side of the oesophagus, through the cranial cavity, and emerging with the oesophagus reach the buccal mass. Here each artery runs below the sub-oesophageal

ganglion, but internal to the neurilemma of this ganglion, i.e., between the neurilemma and the ganglionic substance, and then divides into three branches. One of these supplies the anterior salivary gland (Pl. VI, fig. 50, *S. A.*), the anterior branch supplies the anterior lateral wall of the buccal mass, and a third branch runs ventrally, to supply the ventral posterior portion of the buccal mass (fig. 50, $B_1 A_1$, *B. A.*). Small arteries accompany several of the nerves given off by the sub-oesophageal ganglion. Anterior to the salivary and pharyngeal arteries a second branch is given off which divides into several arteries:—(1) an artery giving off a branch to the funnel (fig. 42, *F. A.*), and then running down on the inner side of the visceral envelope, to end there by splitting up into many smaller branches (fig. 42, *V. E. A.*); (2) a branch which follows the course of the accessory pallial nerve, and so supplies the muscles of the head, and the lateral chamber of the funnel; (3) a branch to the eye (fig. 42, *O. A.*); and (4) a short branch running inwards to the statocyst. The next branch given off by these forks is a second artery to the eye (fig. 42, *O. A.*). A second very fine branch to the anterior part of the funnel is the last branch given off by the two forks of this aorta (fig. 42, $F_1 A_1$).

The Abdominal Aorta is much more slender and less important than the anterior aorta. It arises anteriorly from the ventral wall of the left chamber of the heart, and runs forwards and ventrally. Soon after its origin it gives off a left and right branchial artery. Each of these runs transversely across to the corresponding gill, just dorsal to the kidney sac, and ventral to the auricles (fig. 42, *Bl. A.*). Further along, the abdominal aorta gives off the artery of the ink sac, which runs inwards and forwards to the base of that organ, giving off two

branches to the intestine on its way (Pl. VI, fig. 49, *I. S. A.*, *Int. A.*). The abdominal aorta now curves ventrally, and can be seen on the ventral surface of the visceral mass, between the two diverging anterior ends of the kidneys (Pl. V, fig. 37, *Abd. A.*). After giving off a fairly large branch to the septal muscle (fig. 42, *Sept. A.*), the abdominal aorta runs up alongside the intestine, to end in fine branches on the rectum. In its course it gives off several small intestinal branches, and also a second septal branch (fig. 42, $Sept_1$ A_1). To the left of this is an important branch which terminates on the rectum, after giving off several ramifying branches to the surface of the liver, and a branch to the duct of the ink gland.

The right branchial artery, soon after its origin, gives off a coronary artery to the walls of the ventricle. The left branchial artery, running behind the left kidney sac, soon bifurcates (Pl. VI, fig. 51, *L. Bl. A.*). One of the two forks running along to the oviduct, gives off one or two small branches to the auricle, and at the level of the oviducal gland sends off a recurrent branch which runs down between the water canal and the oviduct, to end in fine branches on the wall of the genital capsule (fig. 51, F_1, *Rec.*). Other branches given off by this fork run to the flask-like portion of the coelom, to the anterior part of the oviduct (fig. 51, *od.*), and to the oviducal gland. The other fork (fig. 51, F_2), after giving off a branch to the genital capsule, runs over and feeds the branchial heart, sends a second branch to the gonad, and ends in a vessel running to the gill tip—alongside the branchial nerve —and supplying each leaflet with nutrient vessels (fig. 51, *Bl. A.*).

The Genital aorta is an independent artery, given off by the postero-dorsal wall of the left chamber of the

ventricle. It runs posteriorly to the genital gland, and ends in several ramifying branches to this organ (fig. 42, *G.A.*).

Venous System.

The blood which has been carried to all parts of the body by the arteries, ultimately passes from the arterial to the venous capillaries, and then flows into a system of veins with definite walls, which carry the de-oxygenated blood back to the gills for aeration. Hence in Eledone, as in most Cephalopods, the circulatory system is highly organised. But still there is one large venous sinus through which blood flows on its return to the gills.

The blood from the arms is collected into two rather wide, superficial vessels, which run one on each side of the arm (Pl. VII, fig. 54, *Arm* V_1, *Arm* V_2, and fig. 52). These lateral veins, externally or aborally receive branches from the aboral part of the arm, and from the web. Orally they receive a series of vessels which alternate with the suckers (Pl. VII, fig. 58). All these veins are superficial. The alternating vessels of one side of the arm anastomose at their origin with those of the other side of that arm (fig. 58). Towards the bases of the arms, these brachial veins join in pairs (figs. 52 and 54), each pair being formed by the neighbouring veins of any two successive arms. Thus eight vessels are formed, which run in the grooves between the arms down to the level of the anterior border of the head (fig. 52, *Br. V.*). On the way they receive numerous branches from the surface of the arms and the web. The posterior ends of these eight vessels are united by a circular vessel of similar width, which embraces the head superficially, just anterior to the eyes. Ventrally this

cephalic vessel joins the anterior vena cava, a wide vessel running over the ventral wall of the cranial cartilage and the liver, down to the kidneys. At the anterior end of these it bifurcates, and each half runs behind the corresponding kidney and soon meets a vessel running in from the middle region of the venous sinus (fig. 52, *Abd. V.*). These two vessels join to form the Lateral Vena Cava of that side, which slants outwards and downwards to the branchial heart, behind the kidney (fig. 52, *L. V. C.*). From the antero-external angle of this heart the blood is led by the afferent branchial vessel to the gill, and is distributed to branches which feed each filament, and becoming aerated as it passes through the thin gill laminae, is collected again into the efferent vessel of the gill. The circular cephalic vessel also receives the venous blood from the superficial muscles of the head and neck by means of small branches which run into its aboral wall (fig. 52, *Ceph. V.* and *Sup. V.*). The ventralmost of the eight interbrachial vessels appears to run into the cephalic vein sometimes to the right and sometimes to the left of the origin of the anterior vena cava. Some superficial muscles must be dissected away to expose the circular vessel fully.

Below the origin of the second ventral interbrachial vessel on each side, a large vessel runs in from the surface of the mantle and the eye (fig. 52, *M.V.*). The origin of this vessel is in the mantle. The whole of the anterior part of the mantle is drained (Pl. VII, fig. 57) by a series of vessels of which only (1) is on the internal surface, while (2, 3 and 4) are external. These four vessels unite to form one, which then receives a branch from the postero-dorsal surface of the eyeball, and one from the corresponding lateral wall of the funnel (fig. 52, F_1V_1). Running up the ventral surface of the

eyeball, just below the skin, this vessel, after receiving small branches on its way, joins the cephalic vessel. The posterior part of the mantle is drained by veins which radiate from a vessel running through the substance of the mantle from its internal surface (figs. 52 and 57, M_1V_1). Here it is joined by the pallial vein, and a vein from the so-called branchial "blood-making gland." The large vessel formed by the union of these three enters the lateral vena cava ventrally just before the latter enters the branchial heart.

The pallial vein runs ventral to the corresponding pallial artery, down from the stellate ganglion towards the branchial heart. It is formed by the union of an anastomosing network of vessels over the ventral surface of the stellate ganglion, a branch from the great lateral muscle, and several branches from the mantle, and on its course receives several small pallial veins (fig. 52, *Pall. V.*).

The Anterior Vena Cava lies on the median ventral surface of the visceral mass and is exposed at the same time as the visceral nerves, by removing the septal muscle and the epithelium covering the visceral mass. It lies to the left of the rectum. Its walls are membranous and semi-transparent. Posteriorly, as mentioned, it ends in two forks which help to form the lateral venae cavae, and anteriorly it originates in a vessel given off from the ventro-posterior wall of the anterior division of the great venous sinus (figs. 52 and 53, S_1V_1). Soon after its origin it bifurcates, and the two halves run round the origin of the internal funnel protractors, and join again below it (fig. 52). Each of these halves receives a vessel which comes from the venous sinus surrounding the white body, optic ganglion, &c., of the eye, pierces the ventral cranial wall obliquely, and then enters the vena cava (fig.

52, *Orb.V.*). Just behind the origin of the funnel protractors are seen two veins from the muscles of the head, and a single ventral vein formed by the union of two running down the back of the funnel (fig. 52, *F.V.*). At the level of the posterior edge of the funnel another branch enters, which is formed by the union of branches from the anterior surface of the visceral envelope and the posterior dorsal funnel wall (fig. 52). Further back the anterior vena cava receives a vessel dorsally from the antero-ventral surface of the liver. This vessel also receives a vein from the wall of the rectum. Ventrally, about the same level, a pair of veins comes in from the funnel depressors, receiving small branches from the visceral envelope on their way. The next branch is from the septal muscle, and is succeeded by another large vein from the liver, entering dorsally, and draining the posterior part of this organ. The final vessel which enters, just before bifurcation, is from the intestine. The small side fig. in fig. 52 illustrates the two valves at the anterior end of the vena cava.

The Lateral Venae Cavae, and the two vessels which run into them from the venous sinus, bear the so-called venous appendages on their posterior walls (fig. 52, *Abd.V.* and *L.V.C.*). These appendages are club-shaped outgrowths of the vessel wall, arranged in five or six irregular rows, the narrow end being that by which they open into the veins. On opening up the lateral vena cava (fig. 56) and examining the posterior internal wall, one sees the circular aperture leading into each venous appendage. This aperture opens into a short vessel whose walls are again pierced by other smaller apertures leading into a smaller series of vessels similarly pierced, and so on, so that each appendage contains in its interior a system of radiating vessels which ultimately opens into

the great vena cava; and the blood in the vena cava thus penetrates into this intricate system in the appendages on its way to the gill. Now externally these appendages are covered by the glandular wall of the kidney, as they encroach on the cavity of the kidney sac. They show many furrows and minute holes on their external surface, which are lined by the glandular kidney epithelium. Hence the blood contained in the vascular network in the appendages comes into intimate connection with the glandular cells of the kidney, and is deprived of its excretory products. The appendages are spongy and yellowish in colour, and show through the ventral transparent wall of the fresh kidney. The two vessels running to the venae cavae from the venous sinus each give off a small branch to the ventricle near their ventral ends (fig. 53, *Cor.V.*). Into the right abdominal vein opens a large vein formed by the union of many branches from the genital gland. Half way along its course this vein receives two lesser vessels from the dorsal region of the visceral envelope, and a branch from the spiral section of the sinus (fig. 53, *V.E.V.*).

The Branchial hearts are purplish glandular organs at the base of each gill, into which the lateral venae cavae open, one at each side (Pl. VII, figs. 52 and 55). This round opening is guarded by two semi-lunar valves which open into the afferent vessel, and prevent the reflux of blood from the gill (Pl. VII, fig. 56). The branchial heart is an organ with very thick spongy walls, composed of soft cellular tissue. The central lumen, however, which these walls enclose is very small. On the internal surface of the wall numerous large and small holes may be seen, which lead into short canals (Pl. VII, fig. 56), from which other smaller passages lead off, and a third series from the second, and so on, the ultimate apertures

leading into small caeca. Hence the wall of the branchial heart is penetrated in every direction by a system of short vessels, which lead ultimately into the lumen of the heart. Therefore venous blood, on entering the organ, penetrates into this system of vessels before it passes on into the afferent vessel which is given off at the antero-external angle of the heart. Cuénot considers that the purplish colour of the branchial heart is due to the purplish concretions found in the cells of which it is composed. By experiment he has proved that these cells are excretory, and therefore that the branchial heart is a glandular organ. The venae cavae, branchial hearts and vessels, and main aortae, as well as the heart, are all rhythmically contractile.

The Venous Sinus extends from behind the mouth to the posterior edge of the stomach, and is divided into three cavities—anterior, central and posterior, the first two of which communicate by important vessels with the large veins. The wall of the sinus is a tough transparent membrane.

1. The anterior division is small and is joined to the middle division by a narrow region, which runs with the oesophagus through the cavity of the ring-like central nervous system (fig. 53). The thin wall becomes adherent to the buccal mass about half-way down its length (fig. 53, *B.M.*), thus forming the anterior boundary of the sinus. Hence the posterior portion of the buccal mass, the anterior salivary glands, and the anterior portion of the oesophagus, are bathed in the blood contained in this division of the venous sinus.

2. The central division is much larger, and narrower in the middle region than at its two extremities, and contains the oesophagus, crop, posterior salivary glands and stomach. However, the liver and ink sac,

enclosed in their common envelope, lie wholly outside and ventral to the sinus (fig. 53, S_2V_2). The anterior aorta penetrates into the latter at the anterior end of the stomach, and runs therein, leaving it only after its anterior bifurcation. Several small infoldings of skin attach the stomach to the wall of the sinus, forming small mesenteries (fig. 53, *Mes.*). The two abdominal veins running from this cavity to the venae cavae, leave it dorsally, one at each side, towards the anterior end of the stomach (fig. 53, *Abd.V.*). Thus the blood from the sinus is drained off by these, and passes direct to the lateral venae cavae, and thence to the gills.

3. The posterior division contains the spiral caecum, which is attached to its wall by several small mesenteries. The anterior wall of this region is common to it and the middle division, but forms only an incomplete septum, allowing free passage of blood, as it is pierced dorsally and ventrally by a row of rather large holes (fig. 53, *Lac.*). The intestine soon after its origin pierces the wall of the middle region, and then bending up over the ventral surface of the liver, lies wholly outside the sinus (fig. 53). The two hepatic ducts pierce the wall of the posterior region, and uniting inside this part of the sinus, enter the spiral caecum. Into the adjacent portions of the venous sinus open small veins from the buccal region, lips, surface of the brain, and the different organs of the alimentary canal which float freely in the sinus.

RESPIRATORY SYSTEM.

(I) Respiration.

The respiration of Eledone appears to agitate the whole of the trunk. Water enters the mantle cavity by the anterior opening during the period of inspiration, when the sides of the body may be seen to swell outwards. At

this time the anterior edge of the funnel curves inwards, and so causes the funnel aperture to become almost completely closed (Pl. II, fig. 7*a*, *f. cl.*). In this sketch it will also be seen that the anterior mantle slit is now widely opened, to allow the water to pass inward (*m.op.*). Inspiration is accompanied by a slight movement upwards and backwards of the whole body. During expiration, the walls of the body contract again, as the amount of water contained in the mantle cavity becomes greatly diminished. This water is, however, bound to go out by the anterior funnel aperture (fig. 7*b*, *f.op.*), for this is now wide open while the mantle slit is tightly closed by the locking apparatus (fig. 7*b*, *m.cl.*). With expiration the body moves slightly downwards and forwards. When a stream of borax carmine was passed in at the mantle aperture, during inspiration, it was passed out again as a red jet, from the anterior funnel opening, during expiration. Thus the way the respiratory water passes was indicated. The stream of water thus ejected is sent out with great force, and disturbs the surrounding water for a considerable distance. There appears to be no constant rate of respiration. After a period of rest, say in the early morning in an aquarium, the rate is sometimes as low as six per minute, while after agitation it increases to sixteen per minute. During the daytime it averaged twelve to fourteen. Smaller specimens appear to breathe rather more rapidly than larger ones. While resting, the tip of the funnel is generally seen protruding either from below the right or the left side of the body (Text fig. I). Every now and then Eledone changes the funnel over from one side to the other, and while so doing the respiratory movements slacken considerably. Often the body will be noticed to heave convulsively, and the respiration to quicken greatly, for a

short time, when there is no apparent cause for disturbance.

(II) Respiratory Mechanism.

1. **Gills.**—Eledone, in common with all the living Cephalopods except *Nautilus*, is Dibranchiate, i.e., it has a single pair of gills. Morphologically these gills represent part of the inner surface of the mantle, which has been specialised for respiratory purposes. They are situated in the mantle cavity, laterally to the visceral mass. When the mantle is cut open, and turned back (as in fig. 11), they may be seen slanting obliquely outwards and upwards from the posterior end of the visceral mass. In fig. 8, which shows the left division of the mantle cavity, only one may be seen. They are attached both to the mantle and to the visceral mass. The gill may be considered as a slender hollow cone, with the apex pointing upwards and outwards. The hollow which forms the base leads into the cavity of the cone, whose walls are formed by the branchial leaflets. The cone is, however, laterally compressed, and is attached to the mantle dorsally, but free ventrally. Along this dorsal attached axis of the gill runs the afferent vessel, while along the free one runs the efferent vessel, so that the plane joining these two axes bisects the gill, and is at right angles to the plane of the mantle. The tip of the cone is situated just posterior to the level of the anus, while the base is slightly behind the urinary papilla. Below this may be seen the branchial heart, which, receiving blood from the body, pumps it on through the afferent vessel to the gill for aeration. Posteriorly the gill is bound to the visceral mass by—(1) The two muscular bands, mentioned in the description of the mantle cavity. The first runs down the ventral side of the efferent vessel, from its tip, and then,

leaving this vessel at the base of the gill, is continued in towards its fellow over the ventral side of the visceral mass. The second, running along the inner side of the afferent vessel from its tip, is inserted with the depressor infundibuli into the mantle, at the anterior end of the mantle cartilage of its side. These two bands of muscle probably serve to deflect the gill, and also by their contraction help the circulation of blood in the vessel each respectively covers. (2) The afferent and efferent vessels, which are continued from the gill into the visceral mass, help to bind them.

The septum which joins the mantle and gill together is triangular in shape. The apex of the triangle points posteriorly, and the base, which is the shortest side, anteriorly. This side is free, and allows the gill to be deflected laterally. That side of the triangle which joins on to the mantle is the longest (Pl. V, fig. 59, *Br. mem.*). The dorsal part of the septum is thin, membranous and transparent in a fresh specimen, but along the edge attached to the gill runs a broad fleshy band, the so-called "spleen," which lies dorsal to the afferent vessel (fig. 59, *Br.gld.*). During life the gills are exceedingly graceful objects, semi-transparent and colourless, and are deflected laterally to and fro in the mantle cavity.

The structure of the gill is exceedingly complex, much more so than the gill of Sepia and other Decapods. The walls of the hollow gill cone are formed by pillars of connective tissue penetrated by blood vessels, and bearing the aerating filaments on their outer surface (Pl. V, fig. 60). There are eleven to thirteen pairs of leaflets in Eledone, the number varying slightly with the size of the specimen. These are arranged in alternate pairs, i.e. the supporting pillars on the external side of the gill alternate with those on the internal surface. Counting

towards the tip, from the base of the gill, the leaflets at first increase in size, the third pair being the largest, and from here they gradually decrease towards the tip. The aerating filaments stretch from the afferent to the efferent vessels, and each leaflet is separated from its neighbours by a slit. Hence water can pass in and out of the cavity of the gill either by the hole at the base, or by the slits between the gill leaflets. Looking through these slits on the external side of the gill, the leaflet of the other side may be seen (fig. 60, *L.* and L_1). This sketch shows a part of the gill from the internal side. At the bottom is the branchial gland, and from it three gill leaflets may be seen running ventrally to the efferent axis of the gill. The centre leaflet has been taken away except for a part at the base, in order to show more clearly the two alternating ones on the opposite side. Posteriorly, these leaflets are attached to the outer side of the afferent vessel which runs up the gill on the inner side of the spleen (Pl. VIII, fig. 63), lessening in size as the gill narrows to the tip. Thus the afferent vessel, covered over by the general lining of the mantle cavity, forms the dorsal wall of the cavity of the gill. Similarly on the outer edge of the gill, the efferent vessel runs from its tip downwards, but a thin sheet of connective tissue (fig. 60, *C.T.*), running inwards into the gill cavity from the efferent axis, along the median plane, separates the efferent vessel from the cavity of the gill, and forms the ventral boundary of the latter (figs. 60 and 63).

The complex gill-leaflets are attached ventrally to this sheet of tissue. First considering each leaflet as a single sheet, it is seen that the aerating portion or filament is on the external side of the attaching pillar, and is consequently bathed in the water of the mantle cavity. Hence blood brought into these filaments for

aeration comes into contact with the constantly changing water supply of the mantle cavity, and is only separated therefrom by the very delicate tissue of the gill filaments. Now, each filament is not a plain sheet, but is crinkled or folded in such a way as to form half cylinders, which alternate with one another as do the leaflets themselves, on each side of the tissue which forms the axis of the filament. This may be understood from the figure where the crinkled filament is shown from the external surface (fig. 62, f_1, f_2, f_3). This sheet of alternating semicylindrical folds does not extend along the full length of the supporting pillar, but only along the anterior two-thirds in the case of all the filaments on the internal side of the gill, while those on the external side bear the aerating folds all along their length, and consequently there are more of these folds here (fig. 60, L_1). The number of aerating folds also varies, of course, with the size of the leaflet.

Now, if we consider each filament as an element of the first order, each of these is crinkled into alternating elements of the second order, these again, in the same way, into elements of the third order, and so on until the eighth series of elements is reached, these ultimate folds being microscopic. Accessory gill leaflets are situated on the vertical septum interior to the efferent vessel, and occur in pairs between successive leaflets (fig. 60, *L.acc.*) all along the gill. Probably they originally were attached to these leaflets, and now have moved slightly away. They equal one of the folds of the true leaflets in size. In shape they are triangular, the apex of the leaflet pointing downwards. Each is crinkled into five or six pairs of secondary elements, whose further structure exactly resembles that of the ordinary secondary element of the gill.

The afferent vessel of the gill runs along the dorsal wall of the branchial cone (Pl. VIII, fig. 63), ventral to the spleen, giving off alternate branches on its way, to the alternating internal and external gill leaflets. Narrowing down with the gill, it runs to its tip. The branch to the leaflet runs in the supporting pillar, and, therefore, on the side next to the gill cavity. Running along to the ventral side of this cavity, it joins another venous vessel, parallel to the main afferent vessel, and forming the ventral wall of the gill cone (fig. 63). Again, each of these vessels to the leaflets or primary elements of the gill, gives off similarly alternating vessels to the secondary elements of the gill (fig. 63, V_{1}, V_{11}), and so on. However, these vessels run along the outer edge of the secondary, tertiary, &c., elements (fig. 62). On the internal surface of the gill, where the leaflets do not bear secondary elements all along their axis, the four lowest folds receive blood from a common vessel (fig. 63). The secondary vessels running up along the outer edge of the corresponding folds, decrease in size and end on the external surface of the gill, at the tip of the fold (fig. 62). As there are eight series of gill elements, and consequently eight series of vessels, the ultimate ones are extremely fine. They open into a venous lacuna in the gill filaments, and the blood which by now is in great part aerated and arterial, is gathered up again into a network of arterial capillaries. Each accessory leaflet receives blood from a vessel given off by the vein parallel to the main afferent vessel, and described above. This vessel runs along the outer surface of the accessory leaflet and divides up exactly as do the branches to the secondary elements of the gill (fig. 63).

The finest arterial capillaries of the efferent vessels are situated in the eighth elements of the gill. Each

fold here sends off rather larger vessels, that form a somewhat coarser meshwork in the seventh element, and so on, till the secondary elements are reached. Now, in the axis of each gill filament, about halfway between the internal and external surfaces, runs the artery from this leaflet, out to the efferent gill vessel (fig. 61, A_1). It originates in branches from the network of vessels in the secondary elements of the gill, and the latter must be turned aside to disclose both the artery and the network (fig. 61, *N.*).

The efferent vessels of the accessory leaflets also originate in a network of capillaries. The meshwork of arteries increases in size in succeeding elements of the gill. Ultimately they open into two vessels:—(*a*) A sinuous vessel common to, and between the two leaflets, and opening into the efferent vessel of the true leaflet between them, but on the opposite side of the gill (fig. 63, and (*b*) A sinuous vessel on the other side of each accessory leaflet, running into the efferent vessel of the leaflet adjacent (fig. 63, 2).

The so-called Spleen or branchial gland of the Cephalopods, would appear to have some intimate connection with the blood, as it is irrigated by both arterial and venous blood, and is placed close to the gill. It is built up of polygonal cells, separated by lacunae of various sizes containing blood (Pl. VI, fig. 63*a*; *b.s.* and *l.b.s.*). There are no true capillary vessels whatsoever. It receives blood: (1) from branches which, coming from the afferent vessel, furnish venous blood (fig. 63, *Aff.v*); and (2) from arteries running down the supporting pillars of the branchial leaflets. These arteries originate in a network formed by the arteries of the accessory gills (fig. 63). This blood mixes in the intercellular lacunae of the branchial gland,

and passing off in the vessel on its inner side, is carried back by a vein to the lateral vena cava (fig. 63, *Br. gld. V.*). This it enters just external to the branchial heart. Probably this gland is connected with the manufacture of the corpuscles of the blood of Eledone—and other Cephalopods.

2. **Skin.**—As the skin of Eledone is very plentifully supplied with capillaries, especially from the venous system (figs. 57 and 58), it is possible that there is also a certain amount of cutaneous respiration.

COELOM.

All Molluscs have a reduced coelom, and a correspondingly dilated haemocoel. Although this phenomenon of "phleboedesis" has not been carried so far as in the Arthropoda, still (1) the coelom has ceased to be a true perivisceral cavity and its main remnants are the pericardium and the genital cavity, which still communicate with one another; and (2) large venous sinuses occur, forming a secondary body cavity.

Whereas in *Sepia* the pericardium and genital cavity are both well developed, and are only separated from one another by an incomplete dorsal septum, in *Eledone* and other Octopoda the pericardial division is greatly modified and reduced. It is represented by a pair of thin-walled, semi-transparent, flask-shaped pouches (Pl. V, fig. 40, *Coel.*), situated laterally, dorsal and posterior to the base of the ureters. Posteriorly each pouch contains the corresponding branchial-heart-appendage, or pericardial gland (fig. 40, *Br. app.*), while anteriorly it opens into the corresponding ureter, by an oval reno-pericardial aperture in the dorsal wall (fig. 40, *R. Pc. ap.*). The genital division of the coelom is well developed in

Eledone, and communicates with the exterior directly by means of the genital ducts and indirectly by means of the so-called "Water Vascular Canals." These are two long slender ducts leading from the genital gland into the pericardium. The right duct is partly shown (fig. 40, *W. V. C.*) where the canal runs dorsal to the right kidney and pericardium, and opens into the latter dorsally, just behind the reno-pericardial opening. In the female there are two symmetrical canals which are long, slender and thick-walled, and open posteriorly into the genital capsule (Pl. V, fig. 39, *W. V. C.* and *ap. int.*) These internal apertures are just exterior to the internal apertures of the oviduct (fig. 39, *l. od. ap. int.*). In the male, however, the right canal alone resembles that of the female in width and position, while the left is much wider—particularly in the region near the genital gland—and opens into the genital capsule quite anteriorly (Text fig. VII, *A.p.* 90). In both sexes the pericardial pouches and the water canals are lined by ciliated epithelium, and as shown (Pl. VI, fig. 51), the water canal follows the course of the sexual duct for the greater part of its length.

EXCRETORY SYSTEM.

The Kidneys—a single pair of large transparent sacs are exposed by stripping off the epithelium which covers the visceral mass. They lie on the postero-ventral surface of the visceral mass, ventral to the heart and posterior to the greater part of the alimentary canal (Pl. V, fig. 37, *R.K.*). The left kidney stretches a little further forward than the right. In young females these sacs may cover the whole postero-ventral surface of the body, but in older females and all males the genital gland pushes them anteriorly and laterally, by its ventral protrusion (fig. 37,

G.). Hence the kidneys tend to diverge posteriorly. They are triangular in shape, the longest side being external. As they are wholly independent of one another, they differ from the kidneys of *Sepia*, where the two are in direct communication. The ureter is situated half way down the external side of the sac, and bears the urinary aperture at the tip (fig. 37, *Ur. p.*). When fresh, the intestine, heart, liver, etc., may be seen through the transparent walls of the urinary sacs. On opening the kidney it is found to contain a thick colourless liquid in which may be seen yellowish accretions of guanin—both the liquid and the guanin being excretory products eliminated from the blood by the glandular cells of the kidney. Roundish colourless corpuscles are found floating in the kidney fluid, and also numbers of the small Mesozoan parasite, *Dicyema mülleri*, in various stages of development (Pl. X, fig. 81). Behind the kidney run the lateral venae cavae, and the two abdominal veins, and where these vessels touch the kidney wall they are produced into the club-shaped venous appendages. The kidney wall, which elsewhere is quite smooth, membranous and non-glandular, is composed of columnar glandular cells where it covers these appendages. As shown (Pl. VII, fig. 56), these "spongy bodies" have their surfaces furrowed by numerous folds and grooves, lined also by the glandular excretory epithelium of the kidney. The visceral mass dorsal to the kidney also protrudes into, and so encroaches on, the cavity of the sac. The ureters are canals about 12 mm. long, and are furrowed longitudinally on their inner surface.

The Pericardial gland is a white gland of somewhat depressed oval form, situated on the inner anterior wall of the branchial heart, and enclosed in the pericardium (fig. 40, *Br. app.*). Numerous folds run inwards from the

free surface of the gland, and in cross section appear as narrow passages. From these passages secondary canals run into the substance of the gland, and end in rounded chambers. Into these chambers open minute caeca, whose walls consist of the glandular excretory cells of the organ. All the above passages are lined with non-glandular cells. Blood entering the branchial heart, fills the passages excavated in its walls, some of which extend into the substance of the adjacent pericardial gland. The blood thus comes into contact with the excretory cells of the branchial heart appendage, and is there deprived of waste matter.

NERVOUS SYSTEM.

All Cephalopods have a highly concentrated nervous system, which reaches its maximum in *Argonauta*, *Octopus* and then *Eledone* ranking next in the series. The typical molluscan ganglia are so closely approximated, and so intimately connected, as to form a peri-oesophageal nerve collar, just behind the buccal mass, and between the eyes (Pl. IX, figs. 70 and 76). In *Eledone*, this collar or "brain" is enclosed in a tubular cartilaginous capsule, the anterior and posterior ends of which are closed by tough membranes. These are pierced for the passage of the oesophagus, posterior salivary duct, pharyngeal arteries, &c. (Pl. X, figs. 85*a* and *b*, and 82, *P.M.*). Round the brain, and separating it from the cranial walls, is found a kind of gelatinous transparent tissue.

Four pairs of ganglia, the cerebral, the brachial, the pedal, and the visceral ganglia, form the brain of Eledone. These pairs of ganglia are, however, very intimately fused together, and although the supra-oesophageal or

cerebral ganglia are distinguishable from the remaining, sub-oesophageal ganglia, yet the three pairs which build up this latter mass cannot be definitely marked off externally one from another. Similarly any two ganglia of a pair are intimately fused, so as to appear like one mass only. The ganglion cells in these ganglia form an external layer round a central fibrous mass.

The Cerebral ganglia form a supra-oesophageal mass oval in dorsal view, triangular when seen laterally (Pl. IX, figs. 76 and 70, *C. G.*). Three transverse grooves mark the ganglionic mass externally into four divisions which increase in size from the front, backwards. The last and largest division is marked with longitudinal alternating bands of white and grey matter, and the regions of the above grooves are also grey. The anterior division of this mass also bears a groove running antero-posteriorly, along its dorsal middle line.

The Brachial ganglia form the anterior third of the sub-oesophageal mass. They exceed in size the pedal ganglia, and together with these form a mass which is morphologically equivalent to the pedal ganglia of other Molluscs (fig. 70, *Br. G.*). As the arms are so greatly developed, while the remaining portion of the foot, the funnel, is comparatively small, so the brachial ganglia exceed the pedal ganglia in size. The former are also connected *above* the oesophagus by a slender supra-oesophageal commissure.

The Pedal ganglia form the central and smallest portion of the sub-oesophageal mass, and innervate the funnel (epipodium) (fig. 70, *Ped. G.*).

The Visceral ganglia lie behind the pedal. According to Pelseneer, there are really two pairs of visceral ganglia—an anterior pair (the pleural ganglia) lying dorsally and giving off the pallial nerves, and a more

ventral pair posterior to these, which give off the visceral nerves (fig. 70, *Ant. Visc. G.* and *Visc. G.*).

Commissures.—Short stout commissures connect the sub- and supra-oesophageal nerve masses. There are two such pairs, the posterior being the broader:—(1) the anterior pair, uniting the cerebral and brachial ganglia, and (2) the posterior pair, uniting the cerebral and viscero-pedal masses.

Nerves.

From the brain are given off numerous pairs of nerves, which innervate the different regions of the body.

A. The nerves given off from the cerebral ganglia are:—(1) Optic, (2) olfactory, (3) labial (4 pairs), (4) buccal, (5) anterior superior ophthalmic nerves, and the motor nerves of the eyeball.

B. The nerves given off from the sub-oesophageal mass are:—(1) Posterior superior ophthalmic, (2) inferior ophthalmic, and the motor nerves of the eyeball, (3) anterior infundibular, (4) posterior infundibular, (5) visceral, (6) pallial, (7) accessory pallial, (8) anterior vena caval, (9) auditory, (10) brachial, (11) interbrachial, and (12) the nerves of the head.

A. (1) **The Optic nerves** are stout, rather short nerves running straight out from the lateral region of the cerebral ganglion at the level of the posterior groove (fig. 70, *Opt. N.*). In section the optic nerve is oval, and piercing the cranial cartilage it enters the orbit and there expands into a large oval optic ganglion from which are given off nerves to the retina (Pl. IX, fig. 71, *R.N.*). These optic ganglia are each greater in bulk than the two supra-oesophageal ganglia, and are about twice as long as they are thick. Internal to the optic ganglion, on the dorsal side of the optic nerve, is a much

smaller oval ganglion (fig. 71, *o.g.*). Chéron termed this the olfactory ganglion, but Zernoff denies its connection with the olfactory organ.

A. (2) **The Olfactory nerves.**—The strands of the olfactory nerve are, at their origin, indistinguishable from those of the optic nerve. They lie ventral to these, however, and run along with them to the optic ganglion. Here they separate, and run on as a separate nerve, which is absolutely independent of and unconnected with Chéron's olfactory ganglion (fig. 71, *olf. N.*). Beyond the separation from the optic nerve it may be seen, running external to the white body, on the internal wall of the orbit (fig. 71, *x.*), where it pierces the wall of the eyeball and then runs over the dorsal posterior wall of the eye to the olfactory pit, which it innervates (Pl. IX, fig. 74, *olf. N.* and *olf. P.*).

A. (3) **Labial nerves.**—These are four pairs of fine nerves, which run out from the anterior edge of the cerebral ganglion and innervate the lip (fig. 76, *a*, *b*, *c*, and *d*). Leaving the cranial cavity, they pierce the membranous wall which closes this cavity anteriorly, and then run over the outer wall of the sinus venosus, which here surrounds the buccal mass, anterior salivary glands, and oesophagus (fig. 76, *S. V.*). Anterior to the sinus venosus, they run over the outer wall of the buccal mass, and so finally reach the lip, where they end in fine branches. The innermost pair of labial nerves (fig. 76, *a*) leave the cerebral ganglion one on each side of the middle line, and running along the outer wall of the sinus venosus, each soon divides into two branches. Reaching the anterior limit of the sinus venosus, each half again gives off several small branches, which end finally in the lip. The second and third pairs have a similar course, the third pair being rather stouter than

the second (fig. 76, *b* and *c*). The fourth pair run forwards and outwards over the wall of the sinus. Thus they cross over the buccal nerves which run forwards and inwards (fig. 76, *d*, and *B.N.*). Each of the two gives off two branches, an inner and an outer. The three branches thus obtained now run over the wall of the sinus to end in the lip.

A. (4) **Buccal Nerves.**—These are two nerves much stouter than the labial. Running from the outer anterior angle of the cerebral ganglion each nerve pierces the anterior cranial wall, and then runs inwards towards the sub-oesophageal ganglion (Pl. VIII, fig. 72, *B.N.*). Arriving at the posterior lateral wall of the buccal mass, this nerve divides into three branches (fig. 72, *D.*, *M.* and *V.*). Of these, the most dorsal runs up to the sub-oesophageal ganglion, the median ends in branches in the buccal wall, while the ventral one curves downwards, and ends similarly in the wall of the buccal mass. The innermost branch given off from this ventral nerve runs towards its fellow from the other side and meets it just below the initial part of the radula sac, swelling here to form a small, oval sub-radular ganglion (fig. 72, *r. b.*).

Ophthalmic Nerves.—To see these it is best to expose the eyes from the dorsal surface by dissecting away the skin and superficial muscles from the back of the head (Pl. IX, fig. 74, *E.*). Thus the muscles which dorsally cover the brain case and the bases of the arms are also exposed (fig. 74, b_1 and *a*). There are three groups of ophthalmic nerves on each side:—(1) three anterior superior, (2) one posterior superior, and (3) three inferior.

A. (5) **The Anterior Superior Ophthalmic** are three fine nerves, which arise dorsal to the origin of the optic

nerve of the corresponding side (fig. 70 *Ant. Sup. oph.*). The most anterior of these pierces the cranial cartilage and so enters the orbit, and runs for a short time along its inner wall. Then, piercing the muscles of the eyeball, it runs external to this out to the eyelid, where it ends in several fine branches (fig. 74, *Ant. Sup. oph.*). The two posterior nerves are motor only. Piercing the cranial wall, and entering the orbit, they are distributed to the dorsal region of the muscles of the eyeball.

B. (1) **The Posterior Superior Ophthalmic** (fig. 74, *Post. Sup. oph.*) is a rather stout nerve, arising from the postero-dorsal angle of the visceral ganglion, anterior to the pallial nerve (fig. 70). Running outwards, this nerve penetrates the cranial wall and so enters the orbit. Here it runs internally to the wall of the orbit, and external to the white body for a short time, and soon expands into a small oval ganglion. Piercing the muscular wall of the eyeball, it runs over its outer surface (fig. 74, *Post. Sup. oph.*), and finally ends in several branches which are distributed to the eyelid.

B. (2) **The Inferior Ophthalmic** are three nerves on each side, of which the posterior is the least and is purely motor, being distributed to the inferior muscular wall of the eyeball. All three nerves, arising from the lateral face of the sub-oesophageal ganglionic mass, rather in front of the median line, run outwards and enter the orbit after piercing the cranial wall. The anterior nerve, after running for a time on the inner wall of the orbit, pierces this, and then runs along its outer wall to the eyelid, where it ends in several fine branches. The median nerve of the three is the largest and has a course similar to that of the posterior superior nerve. Like this, it bears a ganglion, but runs over the antero-inferior surface of the eyeball (fig. 75, *Inf. oph. N.*).

B. (3) **The Anterior Infundibular Nerve** is given off from the ventral surface of the brain, at about its median point (fig. 70, *Ant. Fun. N.*). It is exterior to the nerve of the anterior vena cava and ventral to the auditory nerve. This nerve pierces the ventral wall of the cranial cartilage (fig. 69) anterior to the statocysts. Between the two anterior infundibular nerves is an oval aperture, through which the two forks of the anterior aorta leave the central cavity of the brain, and reach its ventral surface (see arterial system in Section IV). Just before the nerve leaves the cranial cavity it gives off a fine branch which leaves this cavity by an independent hole, and runs to the protractors of the funnel on that side. After leaving the cranial cavity the anterior infundibular nerve gives off a second branch which supplies the posterior dorsal wall of the funnel. Some of its branches run to the wall of the lateral funnel chamber. Soon after, the nerve gives off a third branch to the funnel. This ends in several branches which run to the median wall of the funnel. The anterior infundibular nerve runs on anteriorly, and soon bifurcates, both halves entering the funnel wall, and both supplying eventually the dorsal wall of the funnel. The lower of these two branches soon swells into an oval ganglion, which is about as large as the smaller of the two ganglia on the course of the visceral nerve. From the anterior end of this ganglion several branches run, with the strands from the upper branch, to the dorsal wall of the funnel. The ultimate fine branches in which all these infundibular nerves end form a complete anastomosing network which quite surrounds the funnel walls.

B. (4) **The Posterior Infundibular Nerve** runs out from the brain just exterior to the corresponding visceral

nerve of that side (fig. 70, *Post. Fun. N.*). It is not so stout a nerve as the visceral. Piercing the posterior wall of the cranial cavity, external to this nerve, it runs out to the postero-dorsal wall of the funnel (fig. 69, *Post. Fun. N.*). Next it penetrates the visceral envelope, and runs for a short time on the inner wall of this structure, and then returns to its outer side (Pl. X, fig. 82). Then it runs out to the funnel and innervates its posterior region, splitting into three main forks (fig. 69):—(1) A fine anterior strand which running forwards splits up into several branches innervating the funnel wall; (2) a stouter median branch which ends similarly, just behind the above; and (3) a posterior strand, which innervates the depressor muscle of the funnel.

B. (5) **The Visceral Nerves** are very long and stout. Much of their course may be followed by removing the septal muscle, and also the epithelial cover of the visceral mass, as they run over the ventral surface of the liver. The visceral nerve is given off from the posterior surface of the visceral ganglion, at its external and ventral angle (fig. 70, *Visc. N.*). Piercing the membranous posterior wall of the cranium, it reaches the inner surface of the visceral envelope (fig. 82, *Visc. N.*), courses along the inner surface of the visceral envelope, just to one side of the median line, runs over the anterior surface of the liver, and gains its ventral surface. In fig. 69, *Visc. N.*, it may be seen on the ventral side of the visceral envelope, which it has pierced. It is now separated from its fellow by the anterior vena cava, alongside which the visceral nerve runs for some time. Further back the visceral nerves are also separated by the rectum, which lies on the right side of the vena cava (fig. 69, *R.*). At the level of the anterior edge of the kidney, the visceral nerves begin to slope away from one another, each running out towards

the branchial heart of its side. This slanting course at first causes them to run external to the kidneys, but more posteriorly they run over the kidney sac (fig. 69), and then passing between the ureter and the oviduct—or penis—they gain the branchial heart, and finally end in the branchial nerve which runs up the fleshy axis of the gill (fig. 69, *Bl. N.*). The visceral nerve swells during its course into two ganglia, of which the second is the larger. The first is a small oval ganglion, just anterior to the ureter. From it radiate fine nerves to the oviduct, coelomic canal, flask-like division of the coelom, and the aorta (fig. 69, *g'*). Two other fine nerves are given off, one running down the surface of the kidney to the wall of the genital capsule, while the outer and smaller nerve ends in the kidney wall (fig. 69). The second ganglion is larger, and is about 3 mm. across (fig. 69, *g''*). It is attached to the cord dorsally, and adheres to the wall of the branchial heart. Branches radiate out from its free edge, to the walls of the lateral venae cavae, and the efferent artery. Several branches are also given off to the substance of the branchial heart, and there is a small anterior branch which runs to the muscles of the back. Two longer branches sink down dorsal to the kidney, and end in the back and the genital capsule respectively. Beyond this ganglion the nerve may be called the branchial nerve. It runs along that side of the gill nearest to the visceral mass, just lateral to the afferent blood vessel (fig. 69, *Bl. N.*). It gradually narrows down with the decreasing size of the gill, and swells to a ganglion at the level of each internal lamella of this organ (fig. 69, *Bl. g.*). Each ganglion gives off a nerve which runs down the gill lamella to which it corresponds, and also a second nerve which runs dorsal to the afferent vessel, and so reaching the external side of the gill feeds

the lamella alternating with the internal one. Soon after attaining the ventral surface of the liver, the visceral nerve gives off a large, much-branched nerve to the anterior vena cava. This runs down along the wall of the vessel to about the level where the ink duct enters the visceral mass (fig. 69). A second branch runs out from the main nerve, over the visceral envelope, and ends in small branches to the depressor of the funnel. On its way, this nerve gives off several branches to the visceral envelope, and while that of the right side furnishes a long branch to the bent region of the intestine, that of the left sends a fine branch to the rectum (fig. 69). The visceral nerve, during its course over the liver, gives off many fine branches to that organ, to the ink sac, to the kidney wall, &c. Nerves may also be seen running to the rectum and the septal muscle.

B. (6) **The Pallial Nerve** is a broad flat nerve given off from the posterior dorsal angle of the anterior visceral ganglion (fig. 70, *Pall. N.*). Running posteriorly and outwards, it pierces the membranous posterior cranial wall, and so enters the visceral sac (fig. 82). On entering the visceral sac it runs outwards and posteriorly along the inner wall of the visceral envelope, towards the great lateral muscle, giving several branches to the envelope in its course. Then it runs obliquely through the lateral muscle, to terminate in a large flat triangular star-shaped mass just exterior to this muscle. This "stellate ganglion" controls the movements of the mantle, on the inner surface of which it lies, covered by the internal epithelium of the mantle. In an adult *Eledone* the ganglion is about 6 mm. across, and its surface is smooth. It gives off a radiating series of nerves to the mantle. These nerves are all stout, and after running for part of their course on the internal wall of

the mantle enter its substance, and divide up into smaller branches, which end there, forming a network of nerves throughout this organ. There are about fourteen of these large branches, and also several short nerves which run directly inwards into the mantle substance from that surface of the stellate ganglion which is applied thereto. The two longest radiating branches run down towards the base of the gill, and innervate the posterior part of the mantle (fig. 69). Internal to these longer nerves are two shorter ones which run below the lateral muscle, and then enter the mantle.

B. (7) **The Accessory Pallial** is a rather more slender nerve, given off just dorsal to the pallial (figs. 69 and 70, *Acc. Pall. N.*). It pierces the cranial wall dorsal to the pallial nerve, and runs alongside this for a short time, on the inner surface of the visceral envelope. Next it runs inwards and becomes embedded in the muscles of the head. Here its fibres may be traced to the lateral wall of the funnel and also to the great lateral muscle.

B. (8) **The Nerve of the Anterior Vena Cava** arises just exterior to and behind the anterior funnel nerve (fig. 70, *Ant. V. N.*). It is a fine nerve which, after piercing the ventral wall of the cranial capsule, curves ventrally round the wall of the anterior vena cava (fig. 69), and ends in several fine branches.

B. (9) **The Auditory Nerve** is short and slender, and runs to the auditory organ or statocyst, from its point of origin, just above the anterior funnel nerve (fig. 70, *Aud. N.*). Each auditory nerve running posteriorly enters the statocyst at its interior and dorsal angle, and then runs to the membranous vesicle, ending in two branches, one to the sensory pad and the other to the sensory ridge in that organ. In reality the fibres of

the auditory nerve arise from the cerebral ganglion (Pelseneer).

B. (10) There are eight **Brachial Nerves** given off from the anterior edge of the brachial ganglion (fig. 70, *Br. N.*) which run forwards over the buccal mass, towards the bases of the arms. They run on the outer side of the wall of the sinus venosus and may be seen there as broad flat bands. Between the above wall and these brachial nerves lie the labial nerves, dorsally. Each brachial nerve runs up the centre of an arm, internal to the corresponding brachial artery, and lessening towards the tip of the tapering arm (Pl. IX, fig. 69, and Pl. VIII, fig. 80, *Br. N.*). At the base of the arms, in the region where they are joined on to the cephalic mass, a circular nerve cord joins the eight brachial nerves together (figs. 69 and 80, *N.Circ.*). This cord is of very peculiar structure. Between the nerves it is single, but in the region of the nerves it splits into two cords, of which the anterior joins on to the brachial nerve, while the posterior runs below it (fig. 69). Running up the arm the brachial nerve bears a series of long elliptical ganglia on its oral surface (Pl. IX, fig. 77, *S.G.*). Each ganglion corresponds to a sucker, and gives off two rows of small nerves which run up to innervate these structures (fig. 77, *S. N.*) and also the muscles of the arm. A gelatinous transparent tissue fills the space between the nerve cord and the walls of the cavity containing it.

B. (11) **Interbrachial Nerves.**—Several small nerves given off between the ventralmost brachial nerve and the one above this run out and innervate the bases of the arms. Also between the second and third, and the third and fourth brachial nerve, counting upwards from below, a fine nerve runs out to these muscles (fig. 70, *I.br.*).

B. (12) **Nerves of the Head.**—Just above the dorsal-

most brachial nerve, at its origin, a fine nerve on each side runs outwards to innervate the muscles of the head (fig. 70, H_1).

Visceral Nervous System.

Eledone, like all other Cephalopods, possesses a visceral nervous system. There are two ganglia, one situated near the anterior end of the alimentary canal, and one near the stomach. The two are united by a long nerve which runs down the wall of the oesophagus. Each of them gives off several nerves to the neighbouring parts of the alimentary canal. This system is connected with the central nervous system by means of the buccal nerve *only*.

The Sub-oesophageal Ganglion represents the anterior centre of the visceral system (fig. 72, *Oes. g.*). It is a fairly large, bilaterally symmetrical, flattened ganglion, situated in the acute angle between the buccal mass and the oesophagus. To expose it properly, the anterior salivary gland must be turned forward (Pl. VIII, fig. 72, *s. g.*). Looked at laterally, the ganglion is roughly triangular. The buccal nerves enter it at its posterior external angles (fig. 72, *B. N.*). From the anterior angle the ganglion gives off several nerves. Of these, the lowest enters the buccal mass, the next runs to the anterior salivary gland (fig. 72, *a* and *b* resp.), the third enters the buccal mass (fig. 72, *c.*), the uppermost (fig. 72, *d.*) runs up to the oesophagus, and then anteriorly along its wall to the buccal mass. The posterior edge of the sub-oesophageal ganglion gives off two nerves to the oesophagus. The anterior one is short (fig. 72, *f*), but the posterior one is long and runs down the side of the oesophagus as far as the crop (fig. 72, *g*). Posterior to the crop the left and right nerves of this pair

join, and then this nerve runs along the ventral side of the oesophagus down to the gastric ganglion. These two nerves give off branches to the oesophagus all along their course, and specially important ones alongside the crop.

The Gastric Ganglion is the posterior centre of the visceral nervous system, and lies on the ventral surface of the alimentary canal, just where the intestine and spiral caecum lead out of the stomach. It is triangular, about the size of a wheat grain, and is exposed on turning forward the liver (Pl. V, fig. 38 *a*, and Pl. IX, fig. 73, *G. g.*).

A. From its right upper corner it gives off:—(1) A large nerve which runs up over the ventral surface of the posterior part of the oesophagus, giving off several branches to the wall on its way (fig. 73, *a*), continues its course along the oesophagus, and ends in the sub-oesophageal ganglion as previously described; (2) several short branching nerves to the base of the oesophagus, and to the ventral wall of the stomach (fig. 73, *b*); (3) a large nerve which runs along the groove marking the division between oesophagus and stomach, and gives off small branches on its way, ending by running round the right side of the stomach to its dorsal border (fig. 73, *c*).

B. From the left upper corner are given off:—(1) A large intestinal nerve which runs along to the anus (fig. 73, *e*); (2) several small nerves which end in the walls of the initial part of the intestine (fig. 73, *f*).

C. From the third and lowest angle of the gastric ganglion are given off:—(1) Several branching nerves to the spiral caecum (fig. 73, *g*); (2) two large and several smaller nerves to the paired hepatic ducts (fig. 73, *h*). These run upwards into the liver.

The large intestinal nerve, from analogy with *Sepia*,

gives off a fine branch to the ink gland at the level where the ink duct enters the intestine. It has not, however, been followed in *Eledone*. From the posterior edge of the gastric ganglion are given off several small nerves to the initial part of the intestine and spiral caecum, and also a large branching nerve to the postero-ventral wall of the stomach (fig. 73, *d*).

SENSE ORGANS.

The general surface of the body of Eledone is sensory, the arms in particular forming slender sensory organs. There are, in addition, well developed eyes, organs of equilibration—the statocysts, and the olfactory organs which probably function also as taste organs.

The Eye.

Eledone has a pair of prominent eyes, situated one on each side of the head (Pl. I, fig. 1, *E*.). As in the case of most Cephalopods, they are sessile. In large specimens of *E. cirrosa* the diameter of the eye is about 25 mm. Although it much resembles the vertebrate eye in several respects, i.e., both are vesiculate and both are very complex and remarkably perfect in structure, yet there are many profound differences. The eye of Eledone has no anterior or aqueous chamber, no choroid, and the cells of the retina are different from those of the vertebrate retina. Again, while the Vertebrate has a cerebral eye, that of Eledone originates as an invagination of the epidermis, which later becomes elaborated into retina, iris, &c. Another important point upon which they differ is that while in vertebrates the optic nerve penetrates the retina and enters the retinal cells from the front, in

the Cephalopod the fibres of the optic nerve enter the retinal cells from behind and do not pierce the retina.

The circular external orifice of the eye is small, only about 6·5 mm. in diameter, and is surrounded by the skin of the head, and the muscular sheet which binds the cephalopedal mass together and to the mantle, superficially (Pl. X, figs. 83 and 84, *ext. or.*). This circular rim round the eye forms an eyelid which can completely close over that organ by radial contraction. Dorsally this eyelid is continued over the aperture of the eye as a membranous semilunar transparent fold (Pl. X, figs. 83 and 84, *ps. ext.*). Ventrally another fold is continuous with the eyelid, this fold also being transparent, but lying below the dorsal one mentioned above, and extending further over the eye (figs. 83 and 84, *ps. int.*). These two membranes appear to be only slightly if at all moveable, and through them may be seen the pupil of the eye (Pl. X, fig. 78, *ps. mem.*). Possibly water may penetrate between them and so bathe the lens directly, as in the Oegopsida. These two membranes may be called the external and internal pseudocorneal membranes, the internal being the thinner. Cutting away these two membranes, the metallic deeply pigmented iris is exposed; this iris bounding an oval pupil (fig. 78, *Iris*) which it opens and closes by a dorso-ventral expansion or contraction. Text fig. V shows the various stages of contraction and expansion which occur in the eye of Eledone. When resting, the eye seems to vary from (*a*) to (*d*) without apparent cause. Stage (*a*), however, seems to occur after a rest of long duration, i.e., it is noticed when examining Eledone early in the morning. Stage (*e*) shows the eye opened much more widely, as it is when the animal is disturbed, and (*f*) shows the condition during periods of great fright or agitation.

Looking into the pupil the lens can be seen. This is a spherical ball, built up of concentric layers of a non-cellular, transparent, cuticular, crystalline substance (fig. 78, *L*). Looking down into the pupil the eye appears black, because the dark retina shows through the lens, from behind.

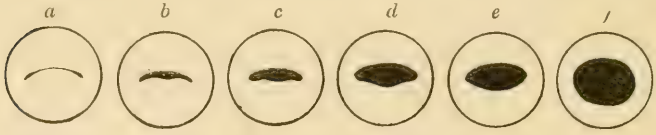

Fig. V. Eye of *E. cirrosa*, showing various stages of dilatation of pupil. x 2.

The eye is enclosed in a cartilaginous cup, that adheres internally to the "skull." This cup is thickest at the base but much thinner at its external edge, which reaches about half-way round the eye (fig. 85 *a*, *orb. C.*). External to the capsule a strong muscular coat is attached which surrounds the eye and extends as far as the lid (fig. 78, *Ext. Musc.*). Internal to the capsule is a second muscular coat, which extends to the border of the pupil, and is more delicate than the first (fig. 78, *Int. Musc.*). The retina, sclerotic, &c., form a roundish, rather depressed chamber that only occupies about one-third of the whole volume of the eye. Behind this chamber is a second much larger one that contains the optic ganglion, which gives off from its external surface a great number of nervous strands to the retina, and the white body (fig. 78, *Opt. G.* and *W. B.*.).

The white body is a glandular mass surrounding the optic ganglion, and consists of three lobes—one large dorsal and two smaller ventral (Text fig. VI). This body has been shown to be the remains of a degenerate portion of the embryonic nervous system,

and possibly is the seat of formation of the blood corpuscles. This, however, is doubtful, as its blood supply, from the arteries of the eye, is very limited. The skin which covers the eyelid, after being reflected over the pseudo-corneal membranes, is continued down the inner surface of the external muscular coat of the eye (fig. 78, *Conjunct.*). Just anterior to the cartilaginous capsule it is reflected on to the globe of the eye, and running up clothes the iris as far as the pupil. Here it is again reflected internally and runs down on the internal surface of the iris, and then over the ciliary body, and then is continued as the external layer of the true cornea. This outer layer of the two-layered cornea thus arises

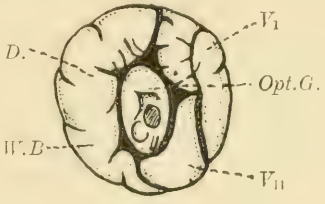

FIG. VI. Diagram showing relation of white body to eye and optic ganglion. × 1.

from the infolded external skin of the head, while the internal layer is the external part of the wall of the optic vesicle, of which the internal part forms the retina. Hence the internal layer of the cornea and the retina are continuous. The two corneal membranes secrete the lens which thus is in two segments, an external smaller one and a larger internal. The external division is a segment of a much larger sphere than is the internal, but the two themselves are of equal area where they adjoin the cornea. They readily separate. The internal segment alone corresponds morphologically with the Gastropod lens. The rest of the ocular cavity is occupied by the vitreous body—a thick, perfectly clear and transparent fluid, contained in a thin membranous sac

(fig. 78, *Vitr.*). The white body and optic ganglion are also contained in a thin-walled sac, which encloses a venous blood sinus—this blood, therefore, bathing these organs.

The optic vesicle is covered posteriorly by a tough semi-cartilaginous sclerotic (fig. 78, *Scl.*). This is iridescent, and reaches to the external border of the ciliary body, which supports the lens. Posteriorly it is pierced by numerous fine holes, which allow the passage of optic nerve strands to the retina. The internal wall of the iris is very darkly pigmented, and raised anteriorly into a circular ridge. While arterial blood is supplied to the eye by two arteries which are given off by the anterior aorta soon after bifurcation, the venous blood is drained off into the above-mentioned venous sinus, and thence passes by a vein through the ventral wall of the skull to the anterior vena cava. As in all Cephalopods, the eye may be adapted for near and distant vision by variation of the distance between the lens and the retina.

The Retina is the most complex part of the eye of *Eledone*. Anteriorly it is continuous with the ciliary body and internal layer of the cornea, and it forms the posterior wall of the optic vesicle. It is very deeply pigmented with a dark brown retinal pigment. Grenacher and Hesse made very careful examinations of the retina of *E. moschata*. The structure (as given by Hesse) of this retina appears to agree with that of *E. cirrosa*, except in one point, which will be mentioned below. The retina consists of a single layer of cells (see Pl. X, fig. 86), which are of two kinds, *retinal* and *limiting* cells. The former are long slender cells, alternating in position with the rather shorter limiting cells (Pl. X, fig. 86, *Ret. C.*; *Lim. C.*). There are three regions in the retinal cell:—(1) The innermost and longest region, where the rods are situated (fig. 86, *Rod.*); (2) the central shortest region,

where most of the characteristic dark brown retinal pigment is collected (fig. 86, *Pig.*); and (3) the basal region, which is external to the basal membrane, and is continued outwards into fine nerve fibres continuous with the nerve cells of the optic ganglion. The nucleus also is found in this region (fig. 85, *Opt. N. f.*; *Ret. N.*).

There are two long slender cuticular rods in each retinal cell. These are crescentic in cross section, and enclose between them the cytoplasm of the cell. By making a cross section of the retina, i.e., at right angles to the length of the cells, it will be seen that the rods are arranged in groups of four, all four belonging to adjacent but separate cells. Hence the two rods of any cell belong to adjacent groups of four rhabdomes.

The limiting cells lie between the visual or retinal cells. They are broadest at the base, and the roundish nucleus is situated here. Also in this region there is an accumulation of pigment granules, corresponding to that in each retinal cell (Pl. X, fig. 86, *Lim. N.*). The limiting cells are shorter than the visual cells, and end just internal to the basal membrane (fig. 86, B_1M_1). This is a membrane of connective tissue, external to the limiting cells therefore, but pierced by the retinal cells. The region below this membrane and between the basal part of the visual cells is occupied by connective tissue and blood vessels (fig. 86, *C. T.*). In the region where the rods are found the limiting cells extend forward only as very fine protoplasmic processes (fig. 86, $Lim_1 C_1$), which are continued as far as, and secrete, the membrana limitans, which covers the internal surface of the retina (fig. 86, *M. L.*).

Hesse has observed in *E. moschata* a fine, somewhat sinuous fibre which runs centrally down each retinal cell, from the basal region, and ends in a minute knob at the

tip. This fibre and knob he considers to be the termination of the nerve in the retinal cell. This continuity has, however, not yet been seen in *E. cirrosa*.

There is in both species a second region where pigment accumulates, towards the internal end of the retinal cell (fig. 86, Pig_1). The pigment here is connected with the larger basal accumulation by a long slender track. This track and internal accumulation surround the nerve fibre and knob, according to Hesse.

In the dark, e.g., at night, the pigment all collects at the base of the cells, but during the daylight much flows up from here, and collects at the apex of the cells, and so protects the delicate visual cells from excess of light.

The Olfactory Organ.

Eledone has one pair of olfactory pits. These are round, of about 3 mm. diameter, and situated just inside the mantle cavity, in the angle between the postero-lateral wall of the funnel and the mantle. Hence they cannot easily be seen in the living specimens. They are shallow pits, lined by horizontally folded epithelium (Pl. X, fig. 66, *olf. P.*).

The epithelial lining consists of two kinds of tall slender cells:—(1) Spindle shaped cells with large nuclei, which are the true olfactory cells, each bearing externally a stiff fine process, while internally they are continued into fibres which run from the olfactory nerve, and having, external to the nucleus, an oval, finely granulated body (Pl. VI, fig. 65, *Olf. cell*). (2) Epithelial cells, of long cylindrical form, which are interspersed among the sensory cells (fig. 65, *Ep. cell*), and have their internal ends drawn out into fine branching processes.

We have no evidence that this organ is really

olfactory in function. More probably it is some kind of taste organ. Its function may be the testing of the water which enters the branchial cavity.

The Auditory Organ.

Eledone has one pair of statocysts, embedded in the ventral wall of the cranial cartilage, and therefore just below the sub-oesophageal nervous mass, between the pedal and visceral ganglia. The membranous statocyst is spherical, with a diameter of 6 mm., and lies in a spherical cavity of somewhat larger dimensions. The organ is attached to its cartilaginous capsule by a network of fine arterial vessels, running to the wall of the vesicle (Pl. VIII, fig. 68, *Aud. caps.*, *Aud. ves.*). The venous blood collects in the cavity of the capsule, and thence passes out to the anterior vena cava, along with the blood from the eye. Dorsally the smooth cartilaginous wall is pierced by the auditory nerve and artery. Internally a thin wall separates the two capsular cavities.

The Statocyst itself is a spherical transparent structure, lined with a flattened epithelium. Its antero-dorsal wall is thickened into an oval pad, whose internal wall is covered with columnar cells, bearing numerous short cilia (fig. 67, *s. d.*). Besides this sensory pad, there is also a sensory ridge, which runs from the former round the dorsal wall of the vesicle, then over the ventral, and finally ends on the dorsal surface (fig. 67, *s. r.*). Between these two sensory regions is a low conical ridge which projects inwards from the wall of the vesicle (fig. 67, *pr.*).

The auditory nerve originates in the cerebral ganglion, runs downwards, and leaving the pedal enters the statocyst dorsally, and bifurcates. One branch ends in the pad, whereas the other supplies the ridge, which is

composed of two longitudinal rows of columnar ciliated cells.

The cavity of the vesicle is filled by a clear transparent fluid. Fitting on the pad internally is a small conical calcareous statolith (fig. 67*a*, and 67, *Stat.*), which is probably secreted by the cells of the pad.

The function of the statocyst is that of equilibration. Experiments in other Cephalopods have shown that destruction of one or both statocysts causes loss of power to balance properly in the water. The description given by Owsjannikow and Kowalevsky of the statocyst of *Octopus* agrees with this organ in *Eledone*. Kölliker has shown that the short blind finger-like canal, running outwards from the wall of the vesicle near the sensory ridge (fig. 67, *K. C.*), is the ciliated remnant of the invagination which gives rise to the auditory pit, seen in the embryos of Cephalopods.

REPRODUCTIVE SYSTEM.

I. Female.

The Ovary occupies the posterior end of the visceral dome. It is a large organ, the size varying with the season, and with the maturity of the specimen. When enlarged, the ovary pushes the kidneys which before partially overlaid it forwards and to one side, thus separating them posteriorly (Pl. V, fig. 37, *G.* and *R. K.*).

The gonad is a whitish oval gland, with a thick tough wall. The ventral region of this wall alone bears the ova, which are suspended from it in racemes. Hence the germinal epithelium of the ovary is confined to this ventral region. There are from 30 to 40 racemes of ova (Pl. V, fig. 39, *ov.*). Elsewhere the wall of the ovary is smooth, with the exception of a much folded and twisted

patch, situated in the middle line (fig. 39, *gldr. p.*). Here there is a thickened region, intersected by many sinuous lines. Above the oviducal apertures the patch is trilobed, while below them it is bilobed and much larger. This raised and folded region forms a frill round each oviducal aperture, the two being separated by a folded ridge (fig. 39, *c. r.*). There are two symmetrical, equally developed oviducts, through which the ova pass from the genital gland to the exterior. They open into the dorsal wall of the genital gland by two closely approximated apertures, one on each side of the middle line (Pl. V, fig. 39, *l. od. ap. int.*). The initial part of their course is best followed by turning aside the ventral wall of the ovary, together with the ova. The oviducts are embedded in the substance of the dorsal wall of the ovary for some distance beyond their origin, and are hence obscured externally (fig. 39, cmb_1). It will be seen that the water vascular canals are similarly embedded in the wall of the ovary for the first part of their course. On reaching the lateral wall of the ovary the two pairs of tubes become free and run round the side of the genital gland to its ventral surface. From this point the oviduct slants obliquely forwards and outwards, dorsal to the kidney, and at the level of the ureter reaches the ventral surface of the visceral mass. About half-way down the duct occurs a whitish oval swelling—the oviducal gland. As shown in fig. 8, the terminal third of the oviduct is visible from the mantle cavity, being only covered by the epithelium of the visceral mass.

All the eggs in any given ovary are at the same stage of maturity. The origin of the ova has not been followed in *Eledone*, and the youngest specimens examined already show the eggs well developed, and surrounded by a nourishing egg follicle. In other Cephalopods the ova

are cells of the germinal wall, which sink below the general epithelium, and then protrude into the ovary, pushing the wall before them until they are completely surrounded by an epithelial layer, several cells thick. The egg itself becomes surrounded by a special nourishing or follicular layer, at the expense of the surrounding cells. With the growth of the ovum, this layer becomes actually folded into the egg substance (Pl. IX, fig. 67*b*, *foll.*), to increase its surface of contact with the ovum. Further protrusion and folding of the germinal wall gives rise to the characteristic racemes (Pl. V, fig. 41, *egg. R.*). Finally the follicle secretes the chorion round the mature ovum, which now escapes, bursting through the covering layers (fig. 67*b*, *C. T.*), and then passing out by the oviduct.

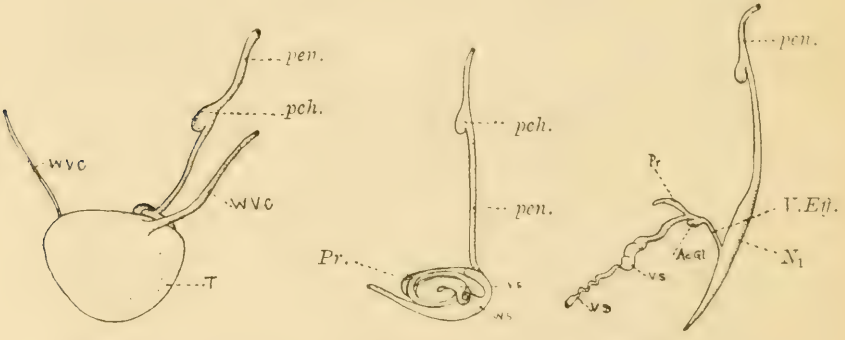

Fig. VII.—A. Fig. VII.—B. Fig. VII.—C.

Fig. VII.—Male reproductive organs of young *E. aldrovandi*. A, from ventral side; B, genital duct as in situ, dorsal view; C, genital duct unravelled to show various regions; x 2.

II. Male.

It is not proposed to give a detailed account of the male genital organs of *Eledone*, as no male specimen of *E. cirrosa* could be obtained. However, the following description of an immature male *E. aldrovandi* will

probably resemble *E. cirrosa* in its general outlines. As in the female, the genital gland is situated posterior to the alimentary canal, at the extreme end of the visceral dome. It is rounded in shape and opens to the exterior by:—(1) Two coelomic canals, right and left, which open anteriorly into the testes (Text fig. VIIA, *W. V. C.*); and (2) one sexual duct, which is the left, the right being atrophied. The hinder portion of this duct is coiled into a spiral mass lying on the left antero-dorsal wall of the genital gland (Text figs. VIIA and B.). The different regions into which it is divided when spread out are shown in Text fig. VIIc. Much of this duct is ciliated internally. The part visible from the mantle cavity resembles in position and appearance the left oviduct of the female (Pl. II, fig. 8, *pen.*).

A narrow winding vas deferens leads off the spermatozoa from the testes (Text fig. VIIc, *V. D.*), and then widens to form the vesicula seminalis. This region and the prostate and accessory glands are concerned in the formation of the spermatophores, i.e., they form a tube round the spermatozoa (Text fig. VIIc, *V. S.*, *Pr.*). Needham's sac (Text fig. VIIc, N_1), into which the spermatophores now pass by a short thin vas efferens, is a store, where they are arranged side by side longitudinally, to await expulsion through the penis. As in the ovary of the female, the ventral wall of the testis is alone germinal.

Spawning.

The eggs examined were spawned by a specimen of *E. cirrosa* in a tank at Plymouth in July, 1903. Since the crabs placed in the tank as food for the Eledones attacked the ova, only two bunches were saved. The ova have not, as yet, been dredged, or taken in the

trawl—possibly they are fastened by the mother amongst rocks in inaccessible places.

The ova of *E. cirrosa* are grouped in characteristic strings during the spawning (Pl. I, fig. 2). One female deposits about 30 of these racemes, each consisting of 25 to 30 eggs, so that the total number spawned is about 800. The whole process of spawning lasts over several days, the racemes being produced at intervals during this time. According to Joubin, *E. aldrovandi* will devour its own spawn if disturbed during the laying process.

The spawn will now be described, so that the order of events in spawning may be understood. The egg itself is enclosed in a semi-transparent horny egg case (fig. 2, *h. c.*), which is secreted by the follicular epithelium before the expulsion of the ovum. Anteriorly this egg case is drawn out into a string for attachment (*egg. st.*). These strings seem first to be twisted together in groups of four to six, and then the latter become intertwisted, thus forming a main central horny axis, which is coated externally by a thin dark layer of horn, and ends in a flat disc which adheres to the glass front of the tank (fig. 2, *A. D.*). The strings of ova are generally attached on or near the glass front of the tank, about a foot from the surface. The actual deposition of the eggs has been observed at the Port Erin Biological Station by Mr. Gravely, of Manchester University, who has kindly furnished me with notes on the process for this Memoir.

For about two hours before the eggs were spawned, the *Eledone* was seen clinging to the glass front of the tank, with the small suckers on the proximal part of the arm extended. Several very violent waves of contraction passed over the body from behind forwards, and several jets of water were directed by the funnel over the

proximal region of the arms and the mouth. The dorsalmost pair of arms was loosely thrown back over the head, and while the ventralmost was pressed against the ventral posterior part of the body, the lateral pairs were thrust into the mantle cavity, and appeared to press vigorously against the visceral mass. Then the arms were all twisted about in the water in an extraordinary spiral manner. After these preliminary indications of great excitement, and preparation for spawning, the Eledone seemed to settle down, the small circumoral suckers were approximated and extended so as to form a closed chamber over the region of the mouth. Then the siphon was inserted into this chamber, and a number of eggs passed in. Next the circumoral suckers began to press the very sticky glutinous substance which accompanied the ova against the glass.

The proximal part of the bunch of eggs, together with the adhesive disc, could now be seen, but the distal part of the bunch was still hidden by the bases of the arms. Next the suckers in this region moved the eggs about and appeared to arrange them in their final condition as described above. When first spawned the eggs have no definite central cord, but appear to be held together merely by the glutinous mass which accompanies them. Then the two ventral arms press the bunch firmly against the glass, and seem to test the firmness of the adhesion. The whole process, after the *Eledone* comes to rest before spawning, occupies from fifteen to twenty minutes.

Eledone very rarely spawns when in captivity—possibly as a result of living under artificial conditions. Hence the fact that it is never kept in aquaria throughout the winter may possibly be explained as the result of becoming egg-bound, as well as of too low a temperature.

At Port Erin, *Eledone* frequently appears to make unsuccessful attempts to spawn, and in the late summer the body swells up greatly and then begins to degenerate, causing death. Possibly this may be due to the absence of males.

The large ova of *E. cirrosa* are oval, and slightly narrower at the tip than at the base, measuring about 19 × 6·5 mm. A large amount of yolk is present, in fine granules. The only egg envelope, or chorion, is transparent and horny, being drawn out into the attaching string anteriorly. At this end also it is pierced by the fine micropyle. The ovum is surrounded by a clear fluid, and the formative protoplasm is aggregated at the anterior end, and round the circumference of the egg cell. No vitelline membrane is present, the follicular epithelium in the ovary secreting the chorion.

During fertilisation it is probable that the male, as in *Octopus*, deposits the spermatophores by means of the hectocotylised arm, in the anterior end of the oviducts. When these spermatophores burst, the free spermatozoa enter the eggs by means of the micropyle. As *Eledone* has no nidamental glands, the egg is not covered by any capsule such as occurs in the case of *Sepia*, or jelly mass as in the egg of *Loligo*. Since in *E. cirrosa* the egg is even larger and more yolk-laden than in *Sepia*, possibly the development may be along similar lines.

No account of the development of *E. cirrosa* can be given, as no living material was obtained, nor has the development of any member of the genus *Eledone* yet been followed out. Drawings of two embryonic stages of *E. aldrovandi* are shown on Plate I. Figure 3 is that of a rather younger embryo than is fig. 4 (after Korschelt), and is drawn from some half-developed embryos kindly given by Mr. E. S. Russell, of Glasgow University.

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EXPLANATION OF PLATES.

Reference Letters.

a. = Base of arm.
a_1 = Arm tip.
an. = Anus.
an. l. = Anal appendage.
ap. int. = Opening of water canal.
au. = Auricle.
au. v., au_1 v_1 = Semilunar valves.
A_1 = Artery of Br. filament.
A_2, A_3., A_4 = Arms.
A and D. = Anterior and dorsal.
A. D. = Adhesive disc.
A. V. C. = Anterior Vena Cava.
Abd. A. = Abdominal Aorta.
Abd. V. = Abdominal Vein.
Ac. Gl. = Accessory gland.
Acc. Pall. N. = Access. Pallial nerve.
Aff. v. = Afferent Branchial vessel.
Ant. A. = Anterior Aorta.
Ant. Fun. N. = Ant. Infundib. nerve.
Ant. Sup. oph. = Ant. Sup. Ophth. nerve.
Ant. V. N. = Nerve of Ant. Vena Cava.
Ant. Visc. G. = Pleural ganglia.
Arm. A. = Brachial artery.
Arm V_1, *Arm* V_2. = Brachial veins.
Aud. caps. = Auditory capsule.
Aud. N. = Auditory nerve.
Aud. ves. = Auditory vesicle.
b. = Degenerate ovum.
b_1 = Muscles over Cranial Cartilage.
b. s. = Blood sinus.
Br. app. 3. *v. r.* = Brachial appendage.
Br. mem. = Branchial membrane.
B. A. = Buccal artery.
B_1 M_1 = Basal membrane.
B. M. = Buccal mass.
B. N. = Buccal nerve.
B. V. = Blood vessel.
Bl. A. = Branchial artery.
Bl. N. = Branchial nerve.
Bl.g. = Branchial ganglion.
Br. A. = Brachial artery.
Br. app. = Pericardial gland.
Br. G. = Brachial ganglion.
Br. gld. = Branchial gland.
Br. gld. V. = Vein of Bran. gland.
Br. ht. = Branchial heart.
Br. M. = Branchial muscle, attaching gill to mantle.
Br. N. = Brachial nerve.
Br. V. = Interbrachial vein.
C. = Cuticular layer.
C. A. = Cephalic artery.
C. G. = Cerebral ganglion.
C. N. S. = Central nervous system.
C. S. = Cartilaginous Stylet.
C. cell. = Cartilage cell.
Ce. = Central tooth of radula.
Ceph. V. = Cephalic vein.
circ. m. = Circular muscle.
Conjunct. = Conjunctiva.
Cor. V. = Coronary veins.
C. T. = Connective tissue.
Cr. C. = Cranial Cartilage.
c. r. = Ridge betw. oviducal. apert.
ch. = Chitinous lining.
Chr. = Chromatophores in dermis.
Cil. B. = Ciliary body.
circ. lid. = Circular eyelid.
Coel. = Pericardial coelom.
coll. = Collar muscle.
cr. = Crop.
Cor. A. = Coronary artery.
Cpdl. mass. = Cephalopedal mass.
Cut. L. = Cuticular lining of oesophagus.
depr. = Depression for spermatophores.
D. = Dermis.
D_1 = Dorsum of heart.
D. M. and V. = Buccal nerve branches.
Du. = Salivary ductule.
E. = Eye.
Eff. A. = Efferent artery.
egg. R. = Egg raceme.
egg. st. = Egg stalk.
emb. = Embryo.
emb_1. = Part of oviduct.
e. m. = Muscular septum.
ep. = Epipodium.
Ep. cell. = Epithelial cell.
Ep. = Epidermis.
Ep. S. = Stylet sac.
Ex. C. L. = Ext. fibrous layer.
Ext. = Ext. musc. of sucker.
Ext. Musc. = Ext. musc. coat of eye.
ext. or. = Ext. orifice of eye.
f. = *Foot.*
f_1, f_2, f_3. = Folds of gill fila'ts.
f. ant. = Ant. funnel opening.
f. cl. = Closed funnel (inspiration).
f.o. = Funnel organ.
f. op. = Open Funnel (expiration).
foll. = Follicular layer.

F. = Funnel.
F_1 = Oviducal artery.
F. A. = Infundibular artery.
F. D. = Depressor muscle of funnel.
F. V. = Infundibular veins.
F. W. = Folded wall, olf. pit.
g. = Gill
gr. = Groove for spermatophores.
g', *g''.* = Ganglia on Visceral nerve.
gr_1 = Groove betw. web and lip.
G. = Genital gland.
G. A. = Genital aorta.
G. g. = Gastric ganglion.
gldr. p. = Glandular region
G. V. = Genital vein.
gld_1 = Indifferent cells.
h. = Head.
h. ap. = Hepato-pancreatic aperture.
h. c. = Horny egg-case.
H. E. = Epithelial covering of hepatic gland.
Hep. A. = Hepatic artery.
H_1 = Nerves to head.
H. = Heart.
H. V. = Hepatic vein.
H. D. = Common Hepatic duct.
i. d. = Ink duct.
int. = Intestine.
i. s. = Ink sac.
I. br. = Interbrachial nerves.
I. C. L. = Internal fibrous layer.
I. p. = Ink duct papilla.
Irid. = Iridocysts in dermis.
I. S. A. = Artery to Ink sac.
I. S. Gr. = Ink sac groove.
I. S. N. = Nerve to Ink sac.
I. S. V. = Vein to Ink sac.
Inf. oph. N. = Infer. Ophth. nerve.
Int. A. = Intestinal artery.
Int. ap. = First part of intestine.
Int. Musc. = Inter. musc. of eye.
Int. V. = Intestinal veins.
I. E. = Iridescent envelope.
i. ep. = Inter. epith. of oesoph.
I. gld. = Ink gland.
J_1 *and J.* = Ventral and dorsal jaws.
K. C. = Kölliker's canal.
l. = Lip.
l_1 = External lip.
l. d. c. = Left dorsal cirrus.
l. b. s. = Larger blood sinus.
l. f. r. = Left funnel ridge.
l. h. d. and r. h. d. = Hepatic ducts.
lid. = Eye lid.
l. m. gr. = Left mantle groove.
l. od. ap. int. = Int. apert. of l. oviduct.
L. = Lens.
L_1 = Branchial leaflets.
Lac. = Apertures in wall betw. S_2 V_2 and S_3 V_3.
Liv. = Liver.
L. acc. = Accessory gill leaflets.
L. Au; *R. Au.* = L. and R. auricles.
L. Bl. A. = Left Branchial artery.
L. F. D. = Left Funnel depressor.
L. F. Pr. = Left Funnel protractor.
L. M. = Lateral muscle.
L. Pall. A. = Left Pallial artery.
L. V. C. = Lateral Vena Cava.
Lim. C. = Limiting cell.
Lim. N. = Nucleus of ditto.
m. = Mouth.
m_1, *m.l.*, *m.p.*, *m.p. ex.* = muscular sheets.
m. cl. = Mantle closed (expiration).
m. op. = Mantle open (inspiration).
m. s. = Muscular septum.
m. s. a. = Attachment of septum.
M_1 = Mantle.
M. C. = Mantle cavity.
M. L. = Limiting membrane.
$M_1M.$ = Muscular mantle.
M. V. = Mantle Veins.
M. W. = Oesophagus wall.
M. ep. = Inner Mantle epithelium.
Matr. = Cartilaginous matrix.
Mem. = Membranous sac.
Mes. = Mesentery.
Mus. = Muscular part of arm.
N_1 = Needham's pouch.
N. = Arterial network in folds of gill filament.
N. A. = Nuchal artery.
N. Circ. = Circular Brachial nerve.
Nuch. M. = Nuchal muscle.
Od. = Oviduct.
od. ap. = Aperture of oviduct.
od. gl. = Oviducal gland.
oes. = Oesophagus.
Oes. g. = Sub-oesophageal ganglion.
o. g. = Oval ganglion.
Olf. cell. = Olfactory cell.
olf. N. = Olfactory nerve.
olf. P. = Olfactory pit.
Opt. G. = Optic ganglion.
Opt. N. = Optic nerve.
Opt. N. f. = Fibres from optic nerve.
opt. N_1 = Nerves to retina.
ov. = Ova.
ov. w. = Wall of ovary.
O. A. = Optic artery.
Oes. A. = Oesophageal artery.
or. = Pyloric aperture.
orb. C. = Orbital cartilage.

orb. V. = Vein to orbital sinus.
p. c. = Polygonal cell.
pad. = Muscular stomach pad.
pch. = Pouch-like dilatation.
pen. = Penis.
ps. ext. = Ext. pseudocorneal memb.
ps. int. = Int. pseudocorneal memb.
ps. mem. = Pseudocorneal membrane.
P. = Pancreas.
P_1 = Terminal suckers of male.
P. C. = Post. communication between mantle cavities.
P. A. = Pancreatic artery.
Pp. = Pupil of eye.
P. M. = Post. membranous wall of brain capsule.
Pall. N. = Pallial nerve.
Pall. V. = Pallial vein.
Ped. G. = Pedal ganglion.
Ph. A. = Pharyngeal artery.
Pig. = Retinal pigment.
Post. Fun. N. = Post. Infundib. nerve.
Post. Sup. oph. = Post. Sup. Ophthalmic nerve.
pr. = Prostate.
r. = Ridge for jaw muscles.
r. b. = Base of radular sac.
r. m. gr. = Right mantle groove.
rad. = Radula.
R. = Rectum.
R. K. = Right Kidney.
R. N. = Retinal nerves.
R. Pall. A. = Right Pallial artery.
R. Pc. ap. = R. reno-pericardial aperture.
R. S. = Radula sac.
R. wall. = Inner wall of oesophagus.
Rec. = Recurrent artery.
Res. = Reservoir.
Ret. = Retina.
Ret. C. = Retinal cell.
Ret. N. = Nucleus of ditto.
S. A. = Salivary artery.
s. d. = Sensory pad.
s. g., s_1 g_1 = Salivary glands.
s. g. d. = Salivary ducts.
sh. = Shell.
s. l. g. = Sub-lingual salivary gland.
sk. = Edge of integument.
s. r. = Sensory ridge.
s. r. o. = Sub-radular organ.
S. = Sucker.
S. a. = Sucker artery.
S. G. = Ganglion supplying suckers.
S. N. = Nerves to sucker.
S. V. = Venous Sinus.
S_1V_1, S_2V_2, S_3V_3. = Divisions of ditto.
S. Vess. = Vein running between successive suckers.
Sept. A. = Septal artery.
Sept. V. = Septal vein.
Sph. = Sphincter of sucker.
St. G. = Stellate ganglion.
scl. = Sclerotic.
Sp. Coe. = Spiral caecum.
St. = Stomach.
Stat. = Statolith.
Str. = Conn. tiss. Stroma.
Sup. V. = Superficial veins of head.
t. = Tongue.
tr. = Secretory trabeculae of Ink gland.
tr. s. = Triangular septum in heart.
T. = Testes.
Tu. = Secretory tubule.
Ur. = Ureter.
Ur. p. = Urinary papilla.
V. = Ventricle.
v. = Trans. valves in spiral caecum.
V. D. = Vas deferens.
V_I, V_{II}. = Secondary Branchial veins.
V_1. = Semilunar valves.
V. app. = Venous appendages.
Visc. A. = Visceral artery.
visc. d. = Visceral dome.
Visc. G. = Visceral ganglia.
Vitr. = Vitreous body.
V. E. = Visceral envelope.
V. Eff. = Vas efferens.
Vasc. N. = Vascular network.
Visc. N. = Visceral nerve.
V. E. A. = Artery to visceral envelope.
V. E. V. = Vein from visceral envelope.
V. S. = Vesicula seminalis.
V_1 S_1 = Sac of vitreous fluid.
W. = Web.
W. B. = White body.
W. V. C. = Water vascular canal.
W. V. C. ap. = Opening of water canal into pericardium.

Plate I.

Fig. 1. Dorsal view of adult female *E. cirrosa*; spirit specimen. × $\frac{5}{8}$.

Fig. 2. Ova of *E. cirrosa*; in formalin. × $\frac{3}{4}$.

Fig. 3. Unhatched embryo of *E. aldrovandi*, right side; in formalin. × 2.

Fig. 4. Older unhatched embryo of *E. aldrovandi*, left side. × 4. (After Korschelt.)

Plate II.

Fig. 5. Oral view of web of adult *E. cirrosa*; spirit specimen. × $\frac{3}{8}$.

Fig. 6. Mouth and initial sucker of arms, showing internal and external lips. × 1.

Fig. 7. (*a*) Eledone from left side, during inspiration; and (*b*) Eledone from left side, during expiration. × $\frac{3}{8}$.

Fig. 8. *E. aldrovandi*, male; left half of mantle cavity. Young specimen. × 1.

Fig. 9. Funnel, showing muscles; integument cut along line (*sk.*), and funnel turned forward ventrally. × $\frac{1}{3}$.

Fig. 9*a*. Ventral view of anterior part of mantle cavity; to show the locking apparatus. × $\frac{1}{3}$.

Fig. 10. Funnel opened to show funnel organ. × $\frac{1}{2}$.

Plate III.

Fig. 11. Mantle cavity from ventral side; showing pallial complex and vertical septum. × $\frac{2}{3}$.

Fig. 12. Visceral mass from ventral side, kidneys removed and ink sac dissected away from liver, and turned forward. × $\frac{1}{2}$.

Fig. 13. Postero-dorsal region of mantle, inner surface; viscera removed, and the funnel depressor and lateral muscles partially dissected away, to show the cartilaginous stylets in situ. Diagrammatic. × $\frac{1}{2}$.

Fig. 14. Cephalopedal mass, dissected to show relation of buccal mass to bases of the arms—from ventral surface. × $\frac{3}{4}$.

Fig. 15. Transverse section of mantle in region of cartilaginous stylet. Highly magnified.

Fig. 16. Right stylet (*a*) dorsal view; (*b*) from right side. × $\frac{3}{4}$.

Plate IV.

Fig. 17. Alimentary canal, dissected out from body, to show relations of various parts; crop turned to the right, buccal mass to the left, and liver forwards. × $\frac{1}{2}$.

Fig. 18. Oesophagus with crop, and stomach; slit open to show ridged chitinous lining of all three regions. Muscular walls of stomach turned back from the chitinous lining. × 1.

Fig. 19. T. S. stomach, showing thickened grinding pads, and corresponding thickened cuticle.

Fig. 20. Buccal mass, from right side. × 1.

Fig. 21. Right posterior salivary gland; inner surface.

Fig. 22. Right anterior salivary gland; inner surface.

Fig. 23. Ventral surface of buccal mass, showing sublingual salivary gland. × 1.

Fig. 24. Sagittal section through buccal mass, and anterior portion of oesophagus. × 1.

Fig. 25. Two rows of teeth from radula; much enlarged.

Fig. 26. Sagittal section of ink sac. × 2.

Fig. 27. Jaws, from left side. × 1.

Fig. 28. Spiral caecum; ventral view, showing entrance of hepato-pancreatic duct. × 1.

Fig. 29. Anal ear (enlarged).

Fig. 30. Inner wall of terminal part rectum, showing aperture of ink duct on dorsal papilla. × 2.

Plate V.

Fig. 33. Transverse section of oesophagus (enlarged).

Fig. 34. Transverse section of tubules of posterior salivary gland.

Fig. 35. Transverse section of tubules of anterior salivary gland.

Fig. 36. Transverse section of secretory tubule of salivary gland, showing secretory cells.

Fig. 37. Kidneys, seen from ventral surface, after removal of visceral envelope. Female. × 1.

Fig. 38. Spiral caecum, opened along columellar edge of spiral, and walls pinned back. The series of transverse valves may be seen, and the internal aperture of the hepato-pancreatic duct. × 1.

Fig. 38*a*. View of viscera, after removing kidney and heart, and turning liver forward—from ventral surface. × $\frac{1}{4}$.

Fig. 39. Ovary, and female genital ducts. The ventral germinal wall has been turned forward anteriorly. × 1.

Fig. 40. Sketch showing relation of pericardial division of coelom to water vascular canal and ureter. Reno-pericardial aperture seen at base of opened ureter. × $\frac{2}{3}$.

Fig. 41. View of portion of germinal wall of ovary, from inner surface, showing attachment of the eggs in racemes. × $\frac{1}{2}$.

Fig. 59. Right gill—ventral view. × 1.

Fig. 60. Portion of gill, from inner surface, showing alternating arrangement of inner and outer leaflets: the central inner leaflet removed. (Enlarged.)

Plate VI.

Fig. 42. Injection of arterial system, showing the distribution of the main brachial, cephalic, pallial, genital and visceral branches. From ventral surface—partly diagrammatic. × $\frac{2}{3}$.

Fig. 44. Amoeboid colourless blood corpuscles.

Figs. 45 & 46. Heart bisected in median antero-posterior plane. Fig. 45 shows dorsal portion from inner surface, and entrance of anterior and genital aortae; also triangular septum. Fig. 46 shows ventral portion from inner surface, with openings of auricles and abdominal aorta. × 1.

Fig. 47. Heart bisected in median dorso-ventral plane, and viewed from cut surface. (*a*) Left half of heart—inner surface, showing triangular septum. (*b*) Right half. × 1.

Fig. 48. Semi-lunar auriculo-ventricular valves, looked at from ventricle. × 1.

Fig. 49. Diagram showing relation of inferior intestinal arteries, and abdominal aorta, to artery of the ink sac. × 1.

Fig. 50. Buccal mass from left side, showing distribution of left pharyngeal artery and branches. × 1.

Fig. 51. Sketch showing distribution of left branchial artery, and its oviducal branch. × $\frac{2}{3}$.

Fig. 63*a*. Sketch showing polygonal cells of branchial gland, and the intercellular blood sinuses.

Fig. 65. Epithelial and olfactory cells lining the olfactory pit. (After Zernoff.)

Fig. 66*a*. Portion of cartilage, showing branching and anastomosing processes of cartilage cells.

Plate VII.

Fig. 52. Figure of venous system, from ventral surface, partly diagrammatic, showing principal cephalic, and pallial veins, and three venae cavae. × $\frac{2}{5}$.

Fig. 53. Large perivisceral blood sinus and its connection with the lateral and anterior venae cavae. Ventral surface. × $\frac{1}{2}$. Partly diagrammatic.

Fig. 54. Two adjacent arms, showing venous vessels and common interbrachial vein. × $\frac{1}{3}$.

Fig. 55. Left branchial heart, showing the branchial appendage or pericardial gland. From ventral surface. × 1.

Fig. 56. Distal portion of lateral vena cava, showing two semi-lunar valves at entrance to branchial heart, and also apertures leading into venous appendages, and into the network of vessels occurring in the spongy wall of the branchial heart. × 1.

Fig. 57. Mantle cut down ventral median line, and opened out flat. The left half is seen from the dorsal surface, after removing the skin. *M. V.* and *M. V*$_1$ represent the two main pallial veins. × $\frac{1}{4}$.

Fig. 58. Portion of arm, showing relation of main veins to the network which drains the arm. × $\frac{2}{3}$.

Plate VIII.

Fig. 31. Ventral view of ink sac, after removal of epithelium covering visceral sac, showing visceral nerves, and nerve artery and vein of ink sac. × $\frac{3}{4}$.

Fig. 32. Ventral view of ink sac, showing veins and arteries injected. The visceral and iridescent envelopes cut open and turned back. × 1.

Fig. 43. Heart from ventral surface, showing paired coronary veins. × 1.

Fig. 61. Gill leaflet, showing network of arteries flowing into the main axial vessel which leads into the efferent artery. × 1.

Fig. 62. Portion of gill filament from external surface, showing terminations of venous vessels of the second order. × 1.

Fig. 63. Portion of gill, from inner surface, showing main arteries and veins injected—second inner filament cut away. Much enlarged.

Fig. 67. Right statocyst, from ventral surface. × 3.

Fig. 67*a*. Statolith, from free surface. Much enlarged.

Fig. 68. Auditory capsules opened to show the statocyst attached to capsule by vascular network. × 1.

Fig. 72. Buccal bulb from left side. The sub-oesophageal ganglion and its branches (*a*—*g*), and the buccal nerve are shown. × 1.

Fig. 79. Longitudinal median vertical section of arm, showing brachial artery and nerve, nerve ganglia corresponding to the suckers, and network of fine arteries and veins which surrounds them. × 1.

Fig. 80. Dissection of dorsal surface of head, showing the circular nerve which unites the brachial nerves, at the bases of the arms. × $\frac{1}{2}$.

Plate IX.

Fig. 69. Ventral dissection of nervous system, partly diagrammatic. Funnel cut open and turned aside, muscular septum removed; the branches from ganglia on visceral nerves are shown only on the right side. × $\frac{2}{3}$.

Fig. 70. Central nervous system, from left side. Slightly enlarged.

Fig. 71. Left optic ganglion and nerve from dorsal surface. × 1.

Fig. 73. Dissection of gastric ganglion and its branches (*a*—*h*). The alimentary canal is seen from the ventral surface.

Fig. 74. Dissection of the superior ophthalmic nerves, and the olfactory nerves from the dorsal surface. The skin and superficial muscles have been dissected away and turned back, showing the muscular coat of the eye, the bases of the arms, and the muscles covering the cranial cartilage. × $\frac{2}{3}$.

Fig. 75. Lateral view of right eye, after dissecting away the superficial muscles and skin. Shows anterior superior and inferior ophthalmic nerves. × $\frac{1}{2}$.

Fig. 76. Buccal mass and central nervous system, dorsal view. The course of the labial (*a*—*d*) and buccal nerves may be seen. × 1.

Fig. 77. Median vertical longitudinal section of arm, showing the ganglion and group of nerves, which supply each sucker.

Fig. 67*b*. Diagrammatic longitudinal section through two ova, showing their mode of attachment to the germinal wall, and also numerous folds of the follicle, which nourishes the developing ovum. In left hand corner is a diagram of an egg in transverse section, showing the infolded follicular membrane.

Plate X.

Fig. 78. Diagram of median vertical section of eye. The whole optic ganglion is drawn in order to show the relation of the retinal nerves to the retina and ganglion. The small figure on the left shows the outer segment of the lens, from the surface which rests on the cornea. × 2.

Fig. 81. Diagram of the parasite *Dicyema mülleri*, found in the kidney fluid of *Eledone cirrosa*. Much enlarged.

Fig. 82. Anterior region of visceral envelope, from inner surface, showing posterior membranous wall of brain case, and various nerves. × $\frac{2}{3}$.

Fig. 83. Eye from external surface, showing lid and pseudocorneal membrane. × 1.

Fig. 84. Median dorso-ventral section through eyelid and pseudocorneal membrane. × 1.

Fig. 85. (*a*) Cranial and orbital cartilages, from dorsal surface. (*b*) The same, ventral view. × $\frac{1}{2}$.

Fig. 86. Vertical section through portion of the retina.

Fig. 64. Dorso-ventral section through olfactory pit, much enlarged, showing the folded sensory wall.

Fig. 66. Right olfactory pit; mantle turned back. × 1.

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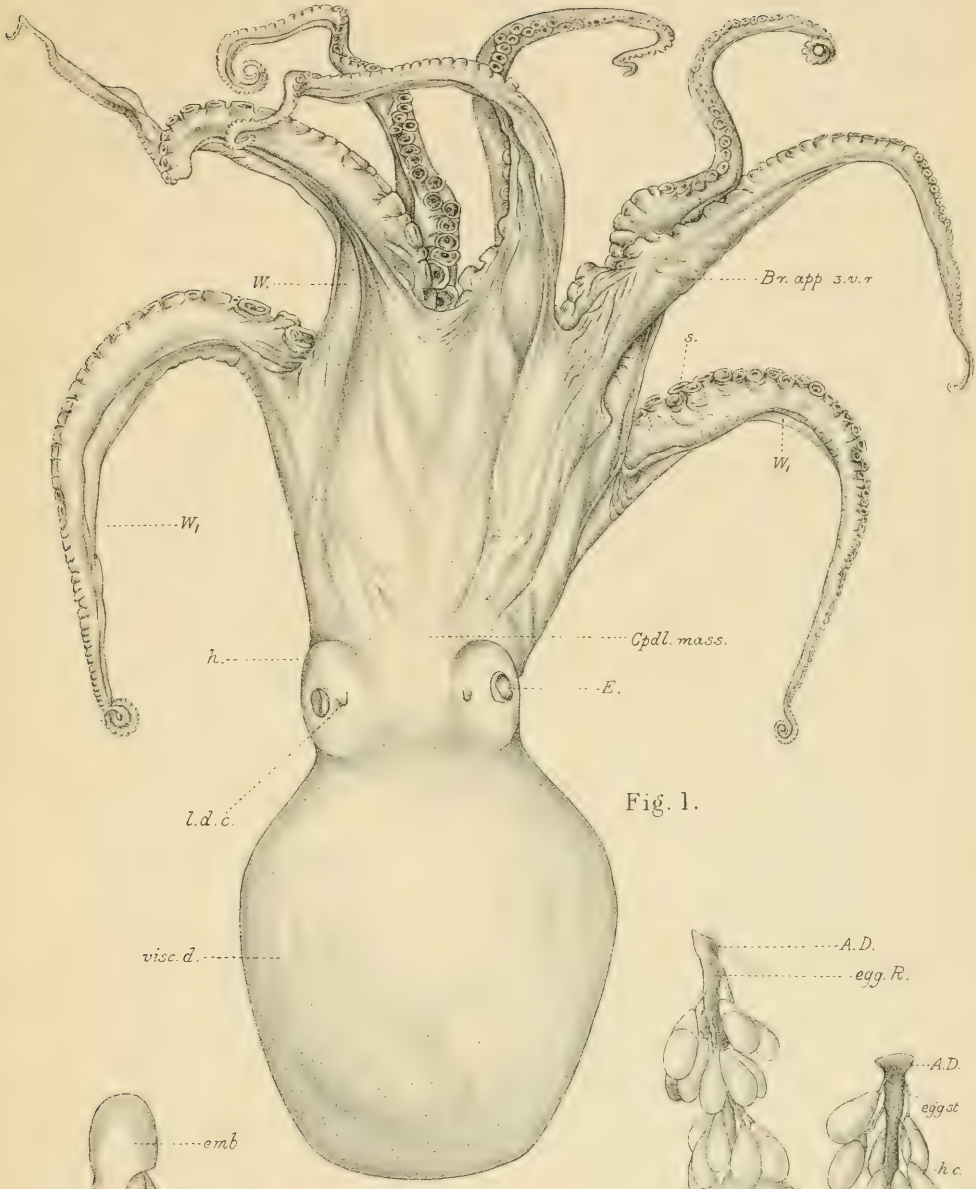

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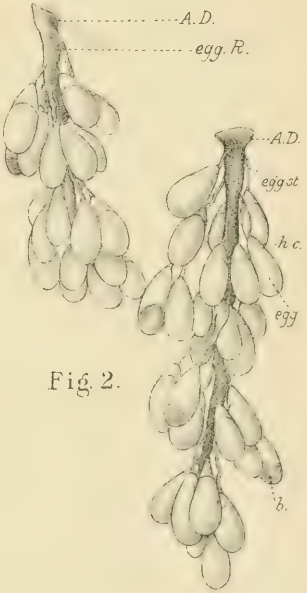

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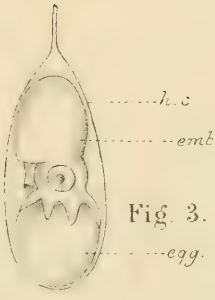

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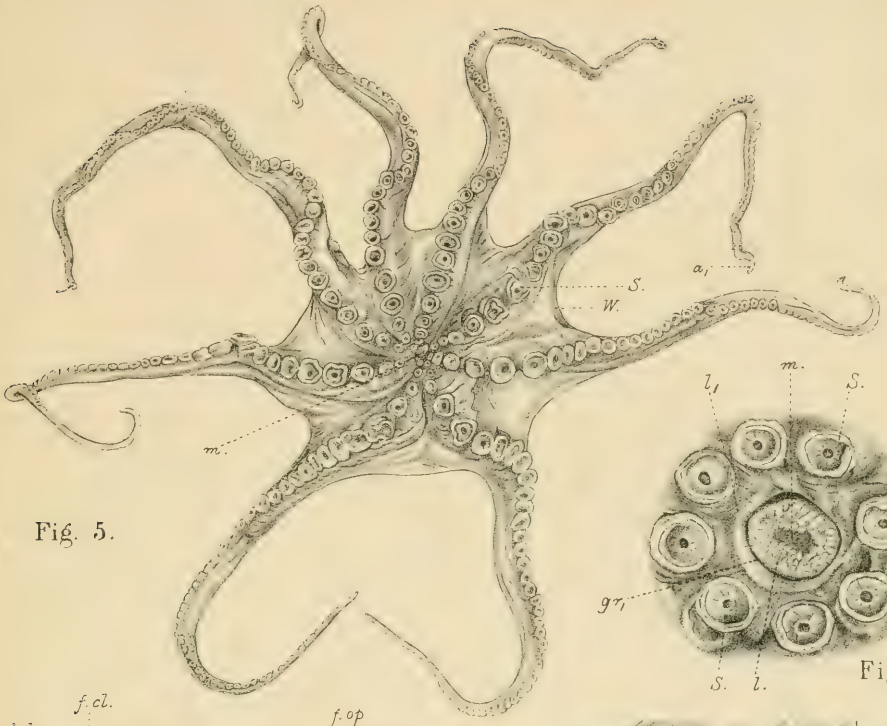

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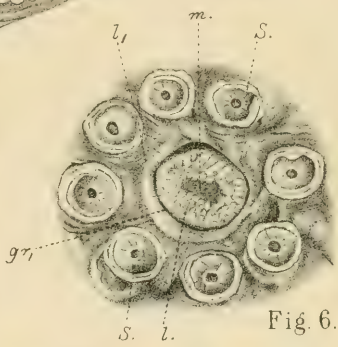

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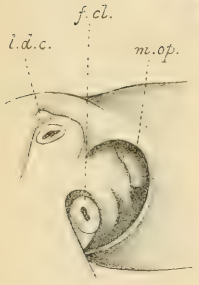

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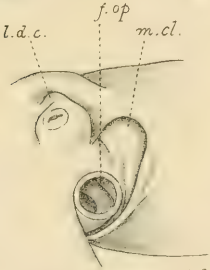

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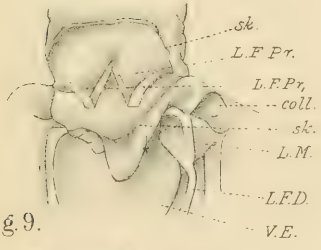

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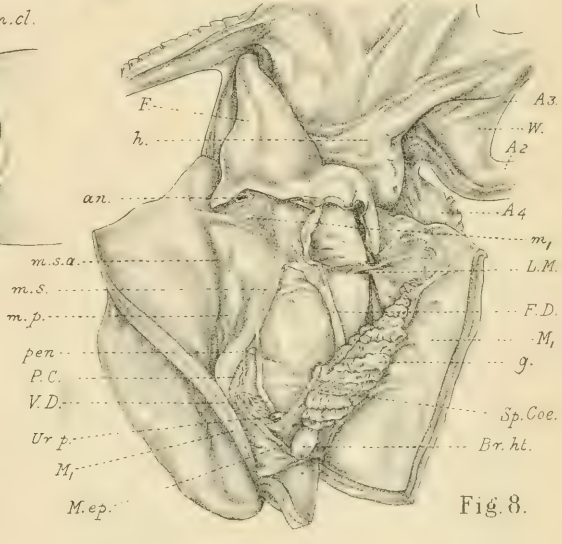

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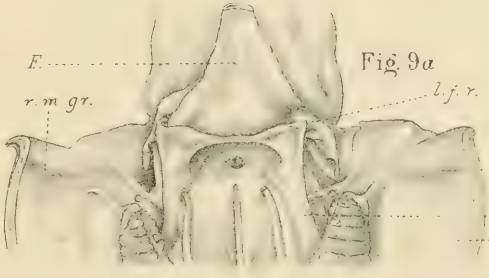

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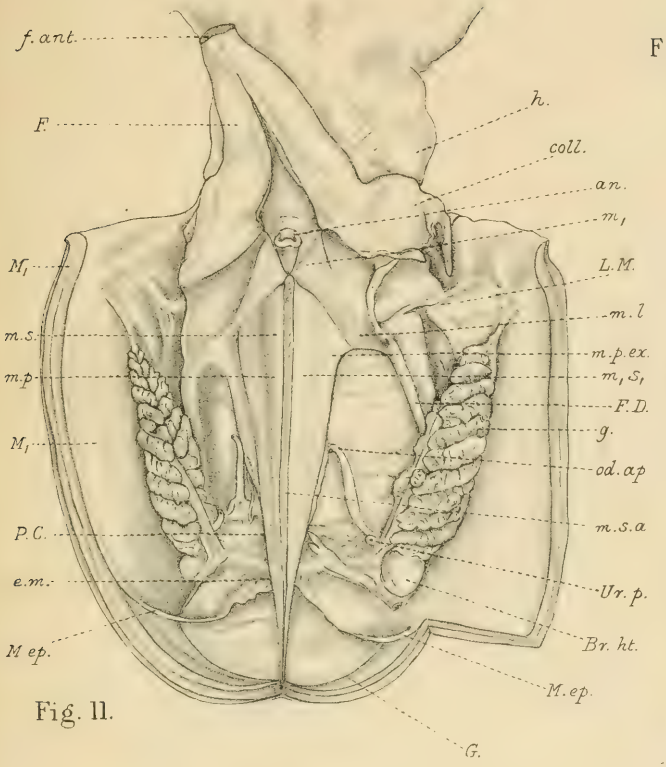

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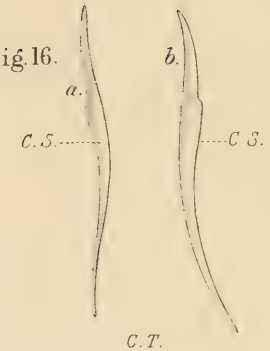

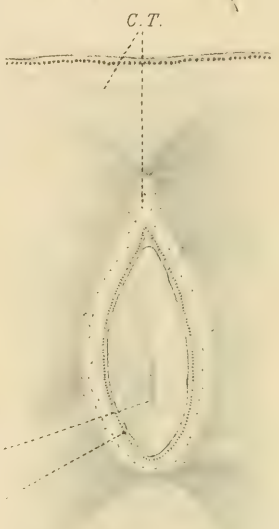

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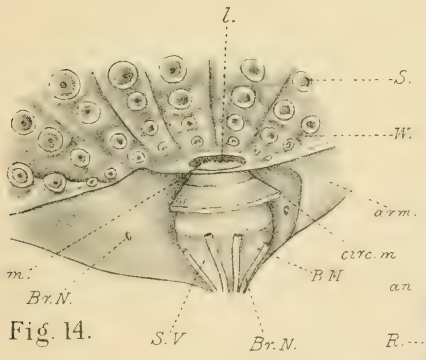

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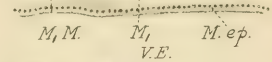

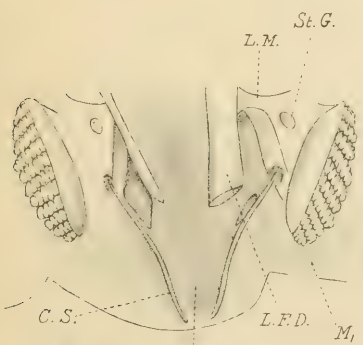

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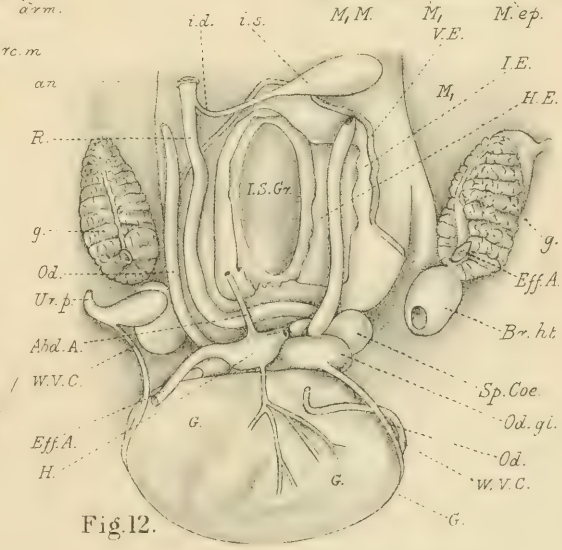

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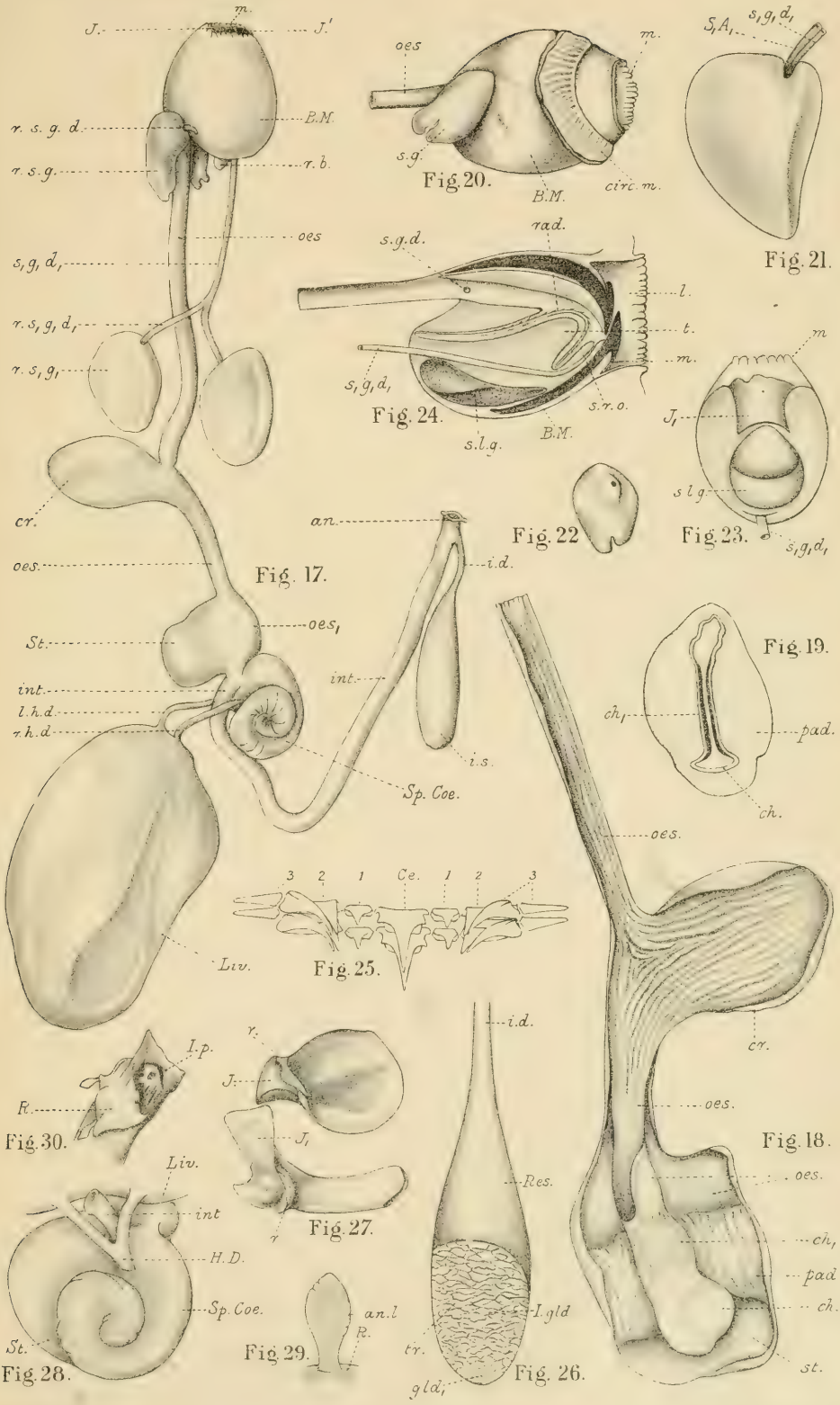

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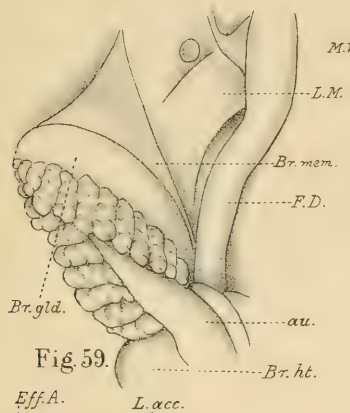

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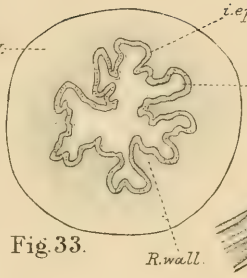

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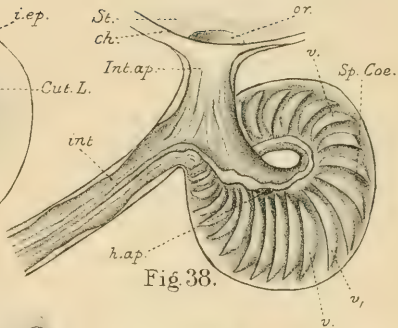

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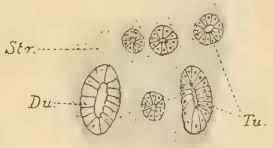

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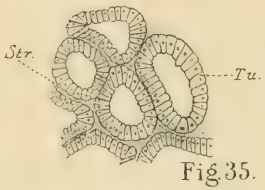

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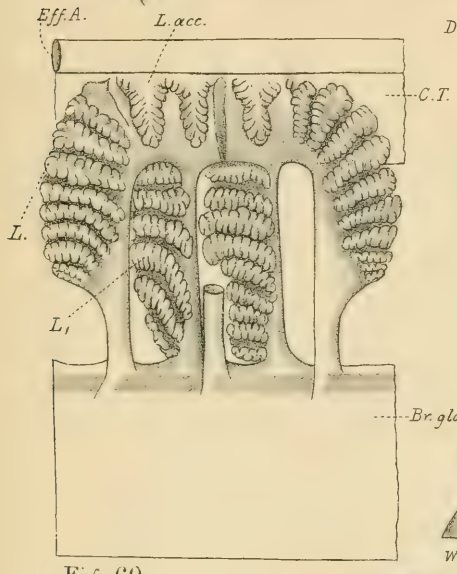

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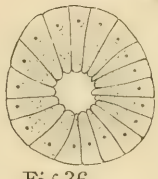
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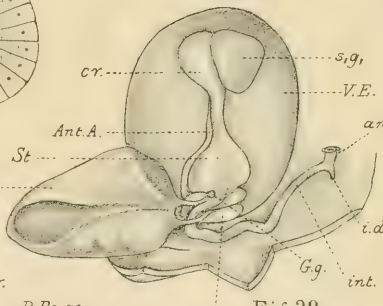

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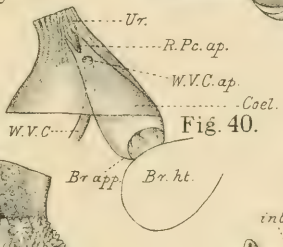

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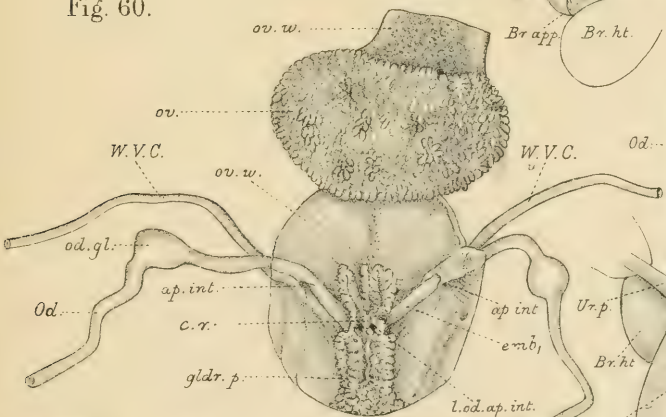

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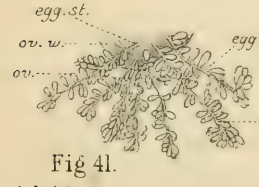

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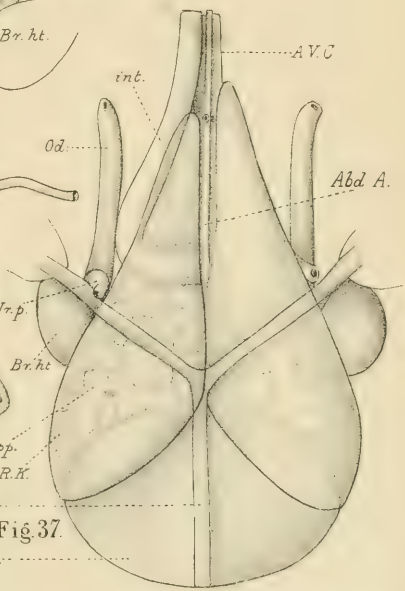

Fig. 37.

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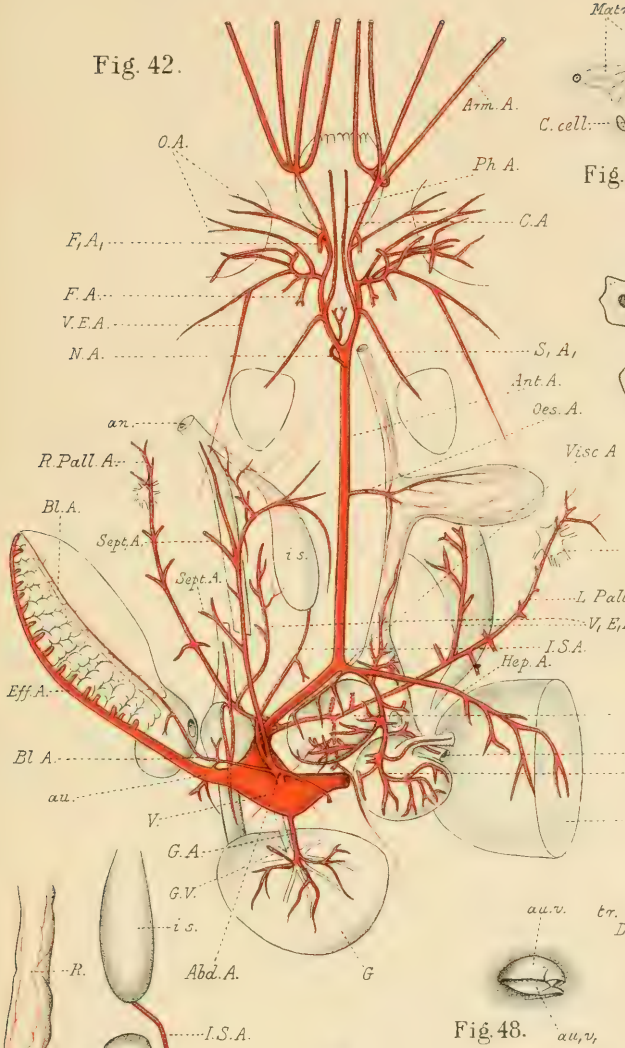

Fig. 49.

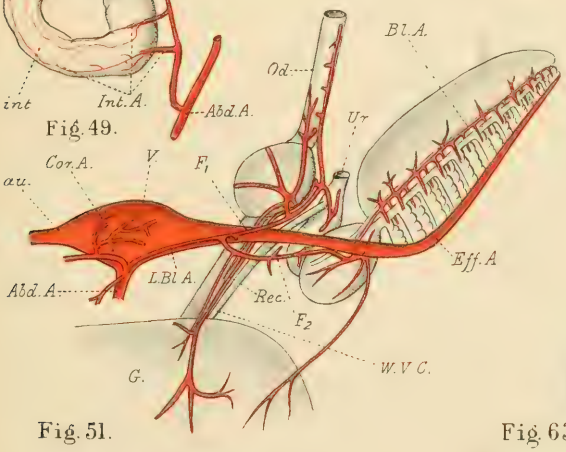

Fig. 51.

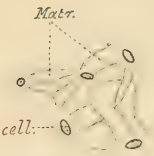

Fig. 66a.

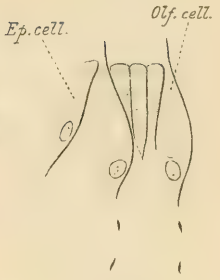

Fig. 65.

Fig. 44.

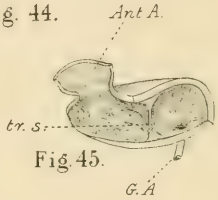

Fig. 45.

Fig. 46.

Fig. 48.

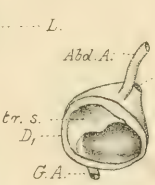

Fig. 47a.

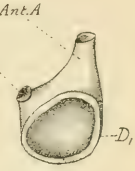

Fig. 47b

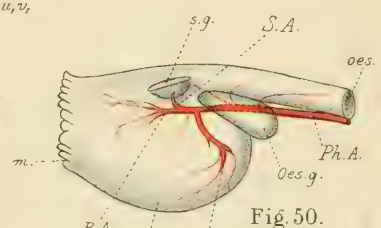

Fig. 50.

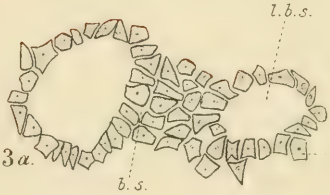

Fig. 63a.

A. I. del.

McFarlane & Erskine, Lith Edin.

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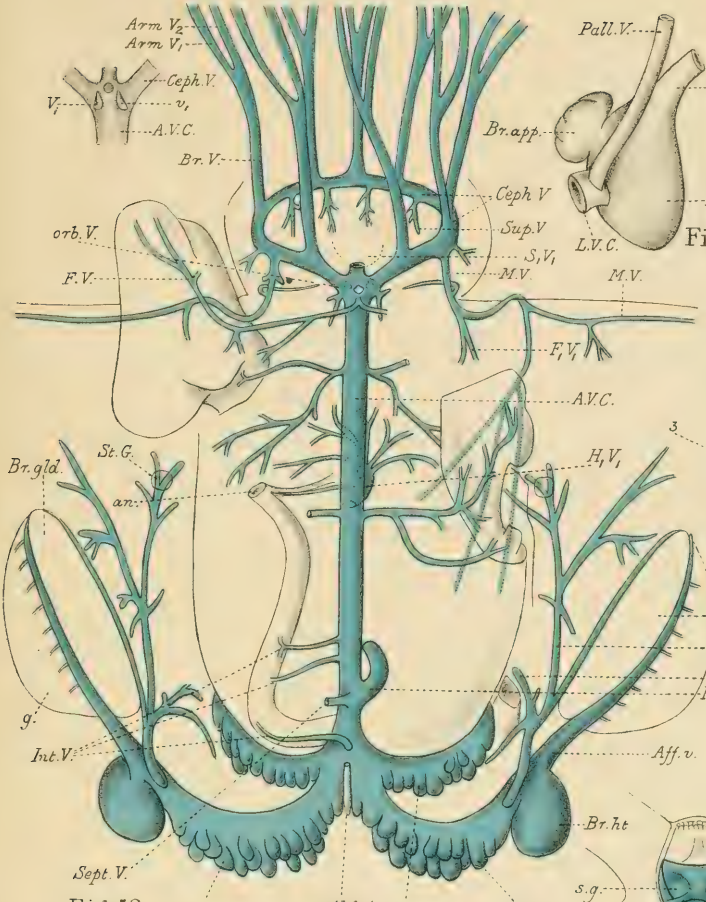


Fig. 52. Fig. 53.

Fig. 55.

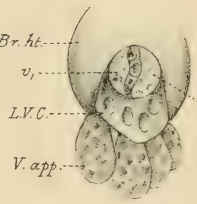


Fig. 56.

Fig. 57.

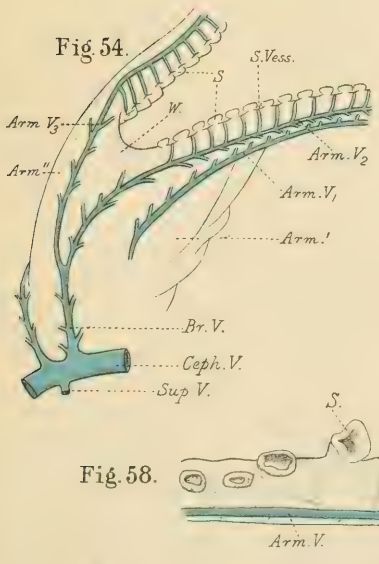


Fig. 54.

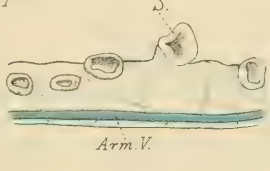


Fig. 58.

A.I. del.

McFarlane & Erskine Lith Edin.

ELEDONE.

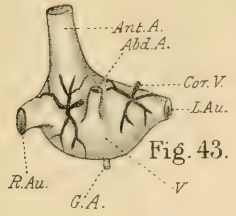


Fig. 43.

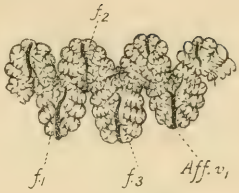


Fig. 62.

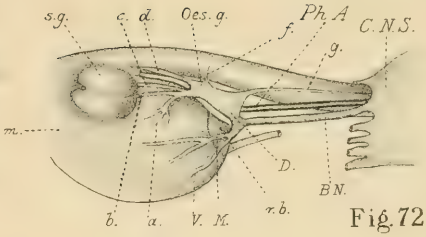


Fig. 72.

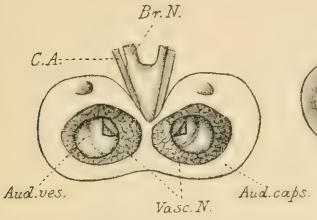


Fig. 68.

Fig. 67a.

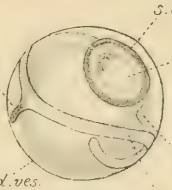


Fig. 67.

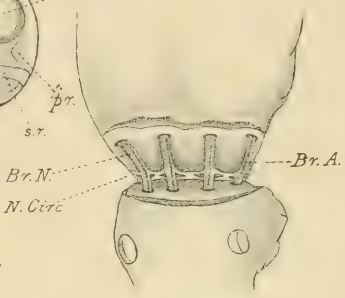


Fig. 80.

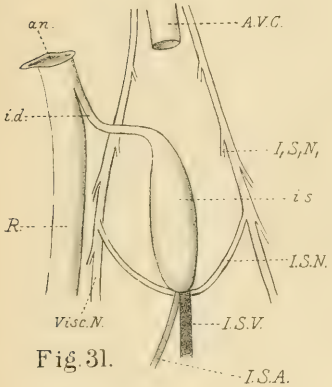


Fig. 31.

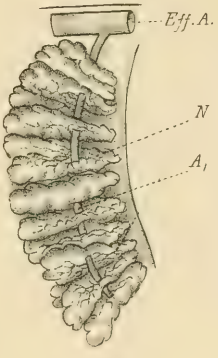


Fig. 61.

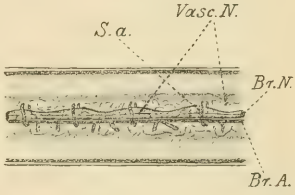


Fig. 79.

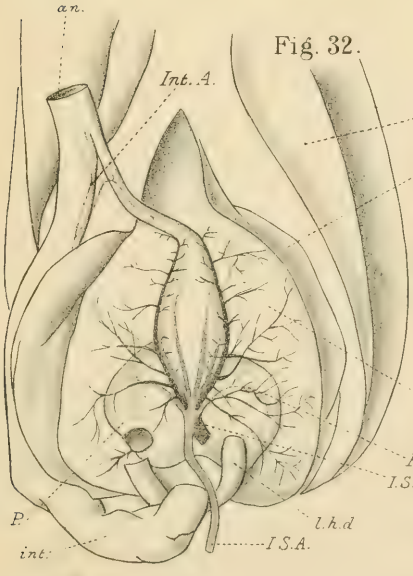


Fig. 32.

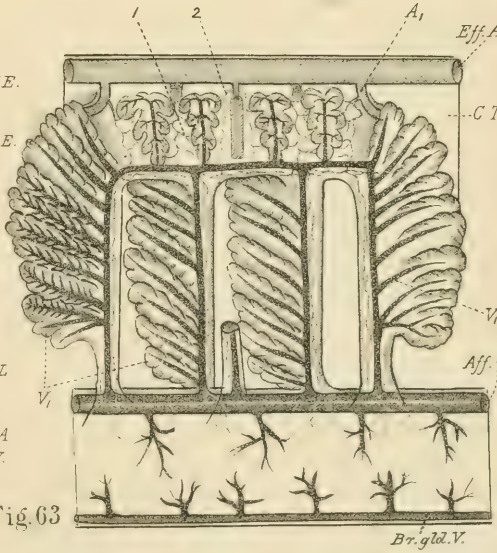


Fig. 63

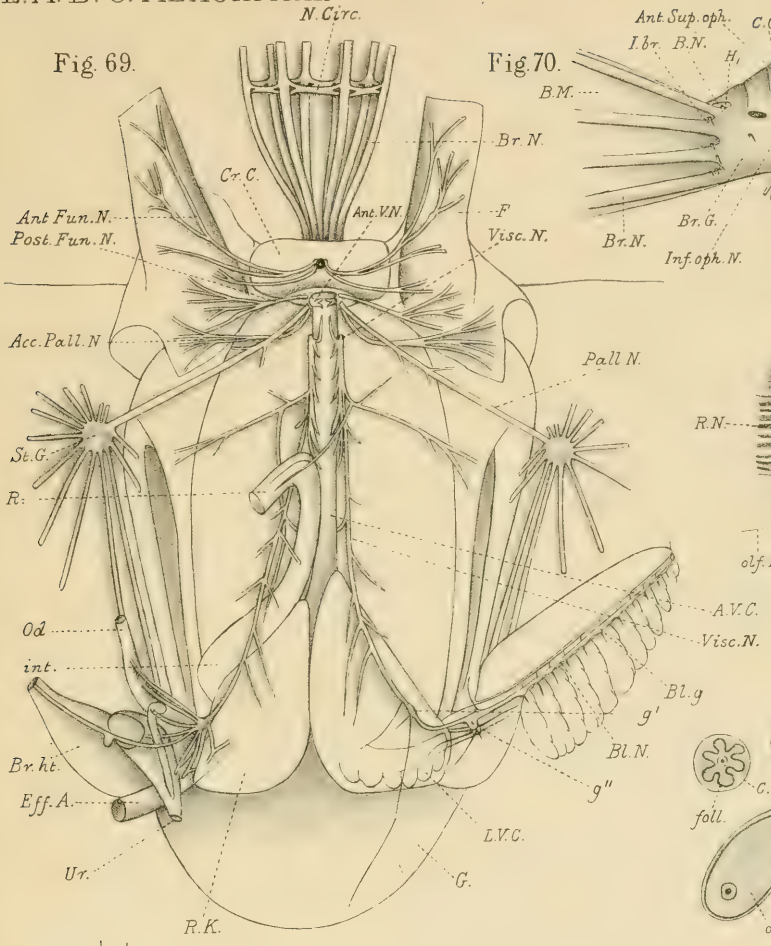


Fig. 69.

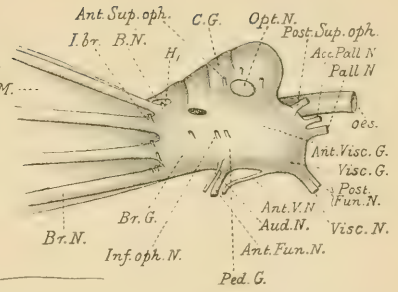


Fig. 70.

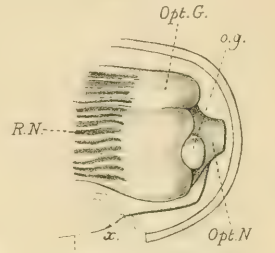


Fig. 71.

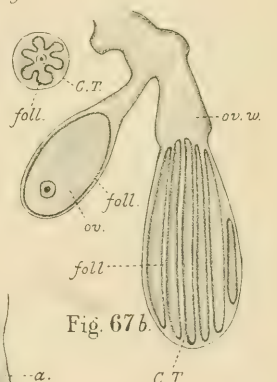


Fig. 67b.

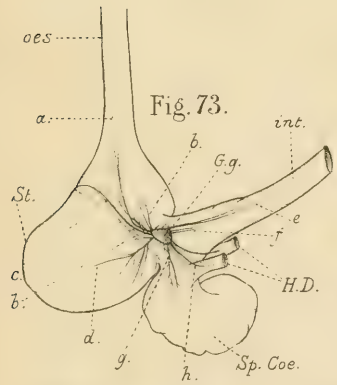
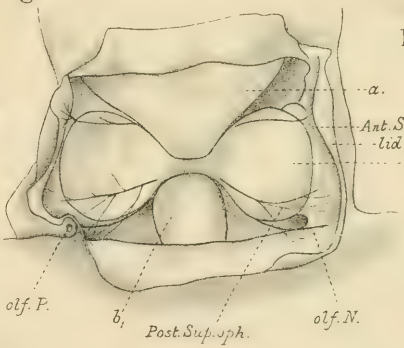


Fig. 73.

Fig. 74.



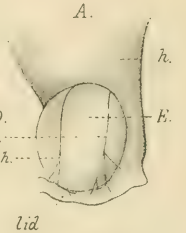


Fig. 75.

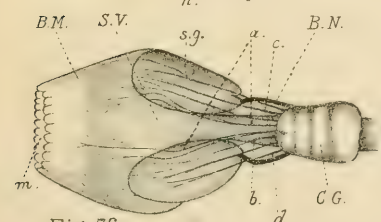


Fig. 76.

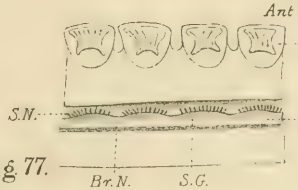


Fig. 77.

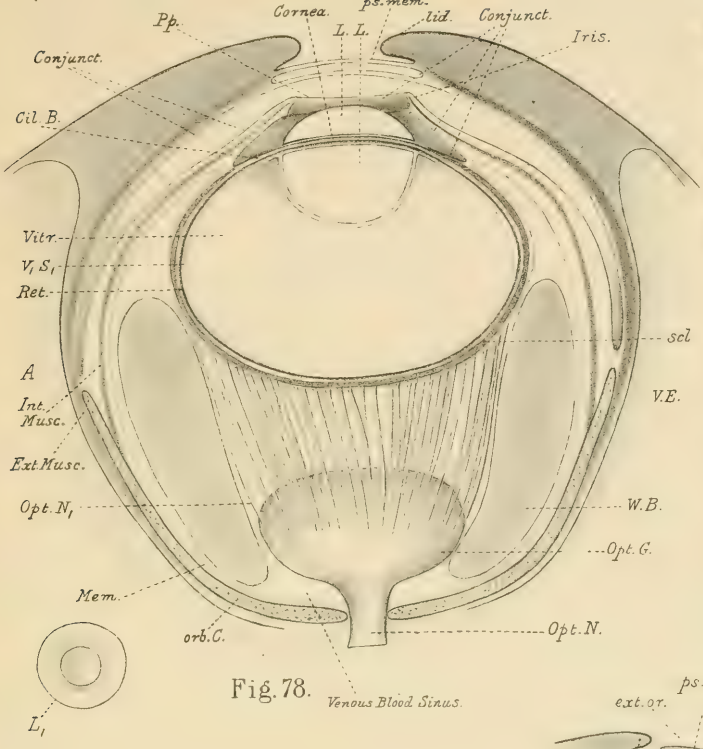


Fig. 78.

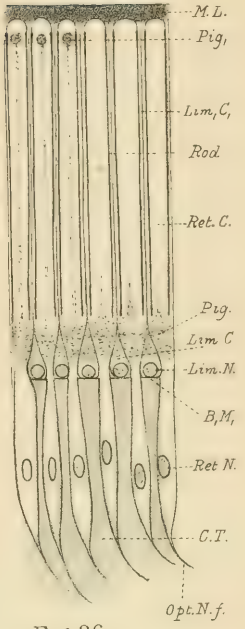


Fig. 86.

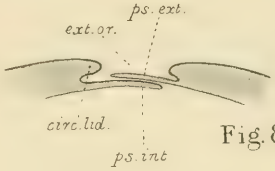


Fig. 84.

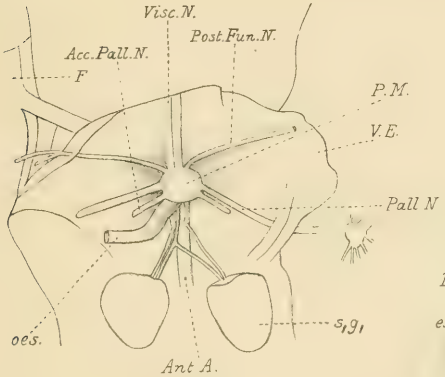


Fig. 82.

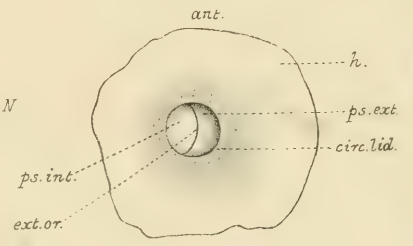


Fig. 83.

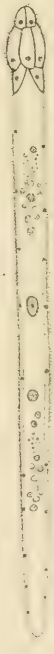


Fig. 81.

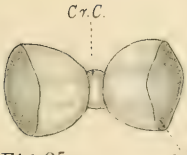


Fig. 85 *a*.

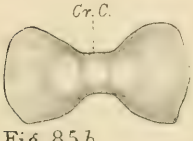


Fig. 85 *b*.

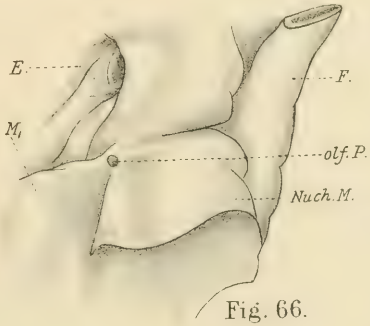


Fig. 66.

Fig. 64.

A.I. del.

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